A SYSTEMATIC STUDY OF THE GENUS *OPHION* IN BRITAIN (HYMENOPTERA, ICHNEUMONIDAE)

by

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Abstract

A taxonomic revision of the British species of *Ophion* is presented, including study of strategic type material. Fourteen species are recognised, two of which are new. Biological and distributional data are summarised as far as the existing data allow. A full discussion of criteria of species recognition is given, and some problems which suggest future experimental work are outlined.

Contents

Introduction

The species of *Ophion* are familiar testaceous Ichneumonids of generally nocturnal habits, frequently taken in light traps. With the exception of two distinctive species, they present unusual taxonomic difficulty — not only due to the close relationship of species one to another, but also owing to the quite exceptional variability of those structural characters which can be used to define species limits. *Ophion* species are parasites of (mainly) lepidopterous larvae (usually Noctuidae), but determinations of the species have been so spurious in the past that a large proportion of the published host records requires further confirmation.

By the time Morley (1915) came to monograph the British species of the genus, a number of species had been proposed by Ratzeburg (1848), Thomson (1888), Kriechbaumer (1879) and Brauns (1889), to add to three "traditional species" of Linnaeus (1758), Fabricius (1798) and Gravenhorst (1829). Most of the later species were inadequately distinguished from *luteus* of Linnaeus, certain of them actually being based upon abnormal colour or structural variants of otherwise "anonymous" species. Morley himself (loc. cit.) described several new species from the British fauna; certain of these were quite valid, although others have been shown to be synonyms of earlier species (see Gauld, 1976). Other keys to European species of the same period (notably that of Schmiedeknecht, 1908) tended to be compilatory in nature and added comparatively little to an understanding of the *luteus* complex. It is to Morley's credit that he correctly dismissed a number of characters used by authors as being unstable within a species, but at the same time, he was unable to find more than a very few new features on which to base his own diagnoses.

With the doubtful exception of Schmiedeknecht's revision of his own earlier key (1936), no real advance was made over Morley until comparatively recently. However, J. F. Perkins of the British Museum (Natural History) had arranged the national collection according to his own assessment of both old and new taxonomic characters, supplemented by study of important type material during the 1930's. Perkins also drew up a manuscript key to the British species of *Ophion* and related genera, which work has been used by several subsequent workers, including the present author. The manuscript was an incomplete study, since its author was working more intensively on his revisions of Ichneumoninae and Pimplinae; the key remained tentative in nature, since Perkins did not include a detailed study of infraspecific variation, nor did

he use all characters which have now come to light. Nevertheless, his work did constitute a great advance over the keys of Morley and Schmiedeknecht.

More recently, Gauld (1973, 1976, 1978) has published several papers on the British species of *Ophion*. He was able to confirm many of the synonyms indicated by the Perkins manuscript and, to some extent, to reassess some of the characters used to define species. Gauld also drew attention to some characters which had not previously been used to define *Ophion* species. At a later stage, Gauld (1978) produced a key to the species of the difficult *luteus-mocsaryi* complex. Oosterbroek (1978), partially following Gauld (loc. cit.), has written an account of the Dutch species, which includes several fresh taxonomic observations. The key given by Gauld now allows identification of a much larger proportion of material than could possibly be gained from the combined works of Morley and Schmiedeknecht, but it will still be found that a dangerously large percentage of specimens will present great difficulty in identification with this key. This fact is due to two reasons:

(1) Gauld relies on the Perkins manuscript key for definition of species. As a consequence, many tentative observations which Perkins made and which were far from being at all fully worked out, are now used by Gauld in much the same taxonomic context as Perkins suggested using them;

(2) Gauld apparently greatly underestimates the variability of many of the characters which he uses; this includes both Perkins characters and certain of those discovered by Gauld himself.

In trying to solve the problems of species definition in the *Ophion luteus* complex, I have found myself adopting a very flexible concept of species limits, since I find that nearly all available characters present an alarming degree of variation — even compared to other Ichneumonid genera which I have studied. I have entirely omitted several characters of authors, which appear to be much too variable to be of any value. I have also placed several others (including some of those studied by Perkins and Gauld) in a more confirmatory than diagnostic context than has hitherto been proposed. In addition, I have brought forward a number of new characters which greatly assist in defining species limits. The key and descriptions given here stress features which I have found to be less variable, supported by other somewhat more plastic variables which nevertheless help confirm species diagnosis. I have usually quoted several characters simultaneously in the key, since this practice makes allowance for variants which may lack one or more of the usual defining features of a species. This accounts for the complexity of the key, but this difficulty is inevitable if accurate determination is to be procured.

Nomenclature

Owing to the inadequacy of many published descriptions, along with the consequent misdetermination of much *Ophion* material by past authors, it has not been possible to present a complete study of synonymy. I have followed what I believe to be the best solution, in dealing principally with the work of more recent authors, with original descriptions, and to some extent with identifications of workers for which material has actually been made available for reexamination. Several type specimens have apparently been lost, and the possibility remains that further research could well bring to light some data which might lead to subsequent adjustment in nomenclature.

Generic synonymy was treated by Townes (1971), and is not repeated here.

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CHARACTERS USED IN DEFINITION OF SPECIES

Head characters

1. The ocellar-ocular interspace, i.e., the distance between a posterior ocellus and the nearest point on the compound eye, compared with the interocellar space (that between the posterior ocelli). Species of the *luteus* complex fall into two sections, one in which the posterior ocelli are nearly or quite in contact with the eyes (e.g. fig. 40) and a second group of species in which there is a distinct, often large ocellar-ocular interspace (see figs. 11, 25). Gauld (1973) terms these species groups the *luteus* and *mocsaryi* groups, respectively, at first freely following the Perkins (MS) definition, later (1978) attempting a modification of this. Unfortunately, intraspecific variation does not allow diagnosis of the two species groups as defined by Gauld. In practice, males of two *mocsaryi* group species very often have a distinct ocellar-ocular interspace, which is not smaller than that found in many specimens in the other species group. Indeed, it is quite frequently larger.

2. The distance between the posterior ocellus and occipital carina — here compared to the maximum (usually apical) width of the first flagellar segment, also with the diameter of a posterior ocellus. These characters seem correlated with the last, but have not previously been used in the taxonomy of *Ophion*.

3. The length of the temple: the maximum length of the temple as seen in lateral view, here compared to the maximum transverse diameter of the compound eye.

4. The stemmaticum: this is the raised area bearing the three ocelli. In *Ophion* it is bounded by sulci of varying definition. The posterior sulcus (see fig. 51) lies behind the posterior ocelli. The lateral sulcus lies between the posterior ocellus and the compound eye and runs forwards to the front ocellus (see fig. 33). The posterior and lateral sulci of the stemmaticum may or may not connect, since the former frequently runs directly into the margin of the compound eye. Sometimes the connection to the eye is through a *stemmatico-ocular line*, which is quite distinct from the sulci bounding the stemmaticum (see fig. 28). The degree of definition of

these sulci has been compared one to another, also with that of the middorsal sulcus, which lies between the posterior ocelli on the middorsal line of the head. — Although variable within species limits, these features are useful in defining species and supraspecific groups within *Ophion*. They have not been used previously in the taxonomy of the genus and are here defined for the first time.

5. The occipital carina. This may be rounded, squared, angled or dipped centrally on the vertex. It is a variable character which nevertheless remains useful in defining species of *Ophion*. Although much used in Ichneumonid taxonomy generally, the form of the occipital carina has not been indicated in previous studies of the present genus.

6. The gena: comparison of genal length with the width of the base of the mandible is a conventional character. It was used by Perkins in his manuscript key to *Ophion*, followed and expanded upon by Gauld. Less precise references to the form of the gena will be found in earlier keys to European *Ophion* species.

7. The postgena and genal inflection: the length of the postgena is here defined as the distance between the mid point of the genal inflection and the nearest point on the compound eye. The genal inflection is that length of hypostomal carina lying between the origin of the latter at the mandible base and its junction with the genal carina. These dimensions are further clarified by fig. 26, and are so defined for the first time. I have compared the length of the postgena with that of the genal inflection, the latter in turn with the width of the mandible base.

8. The compound eyes in frontal view: these may be approximately parallel, divergent (further apart towards mouth than towards vertex), or convergent.

9. Facioclypeal area: delimited above by the line of the antennal sockets, laterally by the margin of the compound eyes, below by the lower edge of the clypeus. The shape of this area is significant and obviously correlated with the last mentioned character. Neither has been used previously in definition of *Ophion* species.

10. The mandibles: of particular significance is the degree of puncturing present on the ventral flange, along the more medial region. Also, the *gape* — here defined as the angle between the two teeth. The *internal angles* of the teeth lie in the excised triangular area where the teeth coalesce, and vary in the extent to which they are defined (compare figs. 14 and 37). Finally,

the basal width of the top edge of the mandible varies in comparison to the maximum width of a tooth (see figs. 45 and 46). Several of these characters are here defined for the first time, none have been used previously in the taxonomy of the genus. Morley (1915) refers to the acute or obtuse nature of the apical teeth of the mandibles, but this feature is too variable within species to be of any real use in definition of taxa.

11. Sculpture of epistoma and orbits: I have compared the distribution of epistomal punctures with those of the facial orbits. This is a variable character, but useful in defining certain species.

12. Maxillary palpi: the last segment is generally distinctly longer than the penultimate, but in certain species these may be of more or less equal length.

The antennae

13. First segment of flagellum: length/width ratios given refer to the maximum (usually apical) width. Gauld (1978) uses the 10th segment in this context, but I do not find the distal segments any less variable than the proximal. In any case, the limits given in Gauld's couplet seven (loc. cit.) are subject to much overlap in actual practice.

14. Number of flagellar segments: this is subject to much variation within a species and has consequently been little used by authors. I have used this character within a more statistical concept of species limits, the numerical nature of variation being naturally suited to this kind of analysis. Gauld follows Perkins in using the number of flagellar segments to define *minutus* and *scutellaris*. With regard to the difficult *luteus — mocsaryi* complex, Oosterbroek (1978) tentatively suggests limits of variation to certain species — limits which must be extended through study of additional material in the present work.

15. Sensilla of first flagellar segment: Gauld (1978) uses this character to define both species and supraspecific groups to some extent. I have not found the limits given by Gauld reliable in practice. Certain species which normally possess sensilla over most of the surface of the first flagellar segment show variation to the extent where they may be nearly or quite absent. Consequently, I have omitted this character from the present study. I shall mention in addition, that certain species which seem particularly well defined with reference to this character are

known from only a small number of specimens. As a general rule, I think it unwise to place too much weight on a character which is seen to be subject to much variation in other species for which suitably large samples have been available for study of intraspecific variation.

The thorax

16. Sculpture: of particular use is the distribution of punctures on the mesopleura, also the form of microsculpture in that region. I have usually only drawn attention to divergence from the normal condition of moderate puncturation and weak microsculpture in descriptions.

17. Colour: most species are largely testaceous in colour. Gauld's key (1978) identifies only *minutus* and *obscuratus* (together with the rare *forticornis*) as having yellow lines on the mesonotum (see fig. 6b), but *obscuratus* frequently lacks these markings and there are other species in which the mesonotum is sometimes vittate (e.g., *parvulus* and *luteus*, also *longigena*).

18. The epicnemium: I have used several new characters from this region, some of which require definition. The *sternal angles* lie ventrally, behind the front coxae, the *pleurosternal angles* at the point where the pleural epicnemium suddenly turns into a more vertical plane. The approximately horizontal portion of the epicnemium lying in the pleurosternal region, in front of the pleurosternal angle, I have termed the *lower sector* of the (pleural) epicnemium. The *upper sector* is that portion of the pleural epicnemium which lies between the pleurosternal angle and that point at which the epicnemium turns forwards to meet the front edge of the mesopleuron. These structures are shown in fig. 2. Characters of particular importance are: (a) shape and angulation of the pleurosternal angle (fig. 2, SP); (b) the degree to which the sternal and pleurosternal angles are aligned along a transverse plane (compare figs. 36 and 49); (c) the ratio of lengths of lower and upper sectors of the pleural epicnemium (see figs. 2, X/Y, 49, 52).

19. Scutellar carinae: in certain species these are more or less frequently well defined. In Gauld's key (1978) the stability of this character has been overestimated. Thomson (1888) used the scutellar carinae in his treatment of *Ophion*, while Morley (1915) correctly assigns a measure of instability to the character. It is nevertheless useful (within limits) for definition of species within the genus.

The wings

20. Distribution of trichiae; Perkins (MS) was first to realise the significance of this character, particularly with reference to the distribution of trichiae on the submedian cell of the forewing. In attempting a reassessment of the reliability of Perkins' observations with reference to infraspecific variation, I find I have been gradually led to the belief that, while the trichiation of the submedian cell remains a useful confirmatory character for a fair proportion of material studied, it is less than reliable when used as a key character. I have regularly met with sizeable population samples in which a species normally having an evenly trichiose submedian cell has the trichiae more sparsely distributed above than below — and *vice versa*. This breaks down the apparent division between *luteus* and those species related to *longigena*, especially since more buccate headed examples of *luteus* are liable to overlap with the *longigena* subgroup, not only in head characters, but also in the distribution of trichiae on the submedian cell. Furthermore, the parallel subdivision of the *mocsaryi* group on the basis of a similar character dichotomy, is prone to a very wide area of overlap. Further investigation of the distribution of trichiae on the forewing however, has led to the discovery of a rather more stable character concerning the degree to which these trichiae extend onto the area immediately beneath the prestigma. The distribution of trichiae in this region is compared with that found elsewhere on the wing; the bare area beneath the stigma (substigmal speculum) may extend beneath the prestigma (compare figs. 39 and 48). Gauld's (1978) use of the trichiation of the submedian cell follows the Perkins manuscript and is unreliable for reasons discussed above.

21. The nervellus: in conventional nomenclature, the nervellus of the hind wing may be broken at, above or below the centre. This is a very unstable character in *Ophion* (see remarks on *costatus* Ratzeburg).

22. Radius of forewing: the radius may be slightly thickened towards the base in certain species. Perkins (MS) drew attention to the non-sinuate radius of *parvulus*. This sinuation occurs on the *second* abscissa (see figs. 38a/b). Venational terminology is that used by past authors working with the Ichneumonidae, rather than the Comstock-Needham system.

Legs

23. Hind leg: the length/width relationships of the hind femur may be very variable within a species, but a trend towards more or less elongate shape can definitely be identified in several species. I do not use actual length: width ratios in descriptions, as these are both variable and difficult to estimate in normal taxonomic practice. Fig. 30 illustrates the usual range of shapes found in the hind femur of *Ophion* species. Gauld (1978) was the first author to draw attention to variation in the form of the hind trochantellus in *Ophion*. He showed that *luteus* and its near allies have a more elongate hind trochantellus than other species. I find I can fully confirm Gauld's observations for all but one *Ophion* species which, due to an unusual variability in respect of this character, will not run correctly in that author's key. In addition to the form of the hind femur and trochantellus, I have found the shape of the hind coxa useful in defining one species.

24. The tibiae: there is useful interspecific variation in the degree of development of the tibial spinules, especially those of the hind tibia (see fig. 41). This character has not been used previously in *Ophion*; it is used in a largely "confirmatory" rather than diagnostic context herein. Perkins, in his manuscript key to *Ophion*, made use of the relative lengths of the apical spurs of the middle tibia in defining certain species. Gauld (1978) follows Perkins, but without critical reappraisal of the variability of the character (see remarks under *O. luteus*).

The propodeum

25. Past authors have made reference to the greater or lesser development of the carinae defining the area superomedia (see fig. 1). This is a variable character, though nonetheless valid, providing other features are taken into consideration at the same time. Of rather more use as a taxonomic character is the degree of development of the carina lateralis in relation to that of the other, more dorsal propodeal carinae (see figs. 43 and 50). This is an easy character to appreciate and it is rather less variable within a species than other propodeal features. Curiously enough, it has been overlooked by previous authors who have worked on *Ophion*.

The abdomen

26. The most useful character I have found

on the abdomen relates to the relative position of the petiolar spiracles and the ventral membrane of the same segment. This simple character has also been overlooked by authors (see figs. 35 and 43). — Morley (1915) refers to the degree of basal constriction of the third tergite as a species level character in *Ophion*, but I have not found this at all stable within a species. — A preliminary study of the male genital sclerites was also made. Some potentially useful characters were found, but it would not have been possible to obtain sufficient material for dissection with some of the less common species. Since infraspecific variation could not therefore be fully assessed, genitalic characters have been left aside in this revision. It is often quite wrongly assumed that these structures possess some special property whereby they are excepted from the necessity of consideration of stability; personal experience suggests that this is far from being the case.

Criteria of species limits

In any taxonomically difficult species group, there is bound to be controversy surrounding the selection of criteria for species recognition. From a practical as well as theoretical standpoint, these difficulties are likely to present their greatest obstacle within what can be termed *close species pairs*. In purely phenetic terms, a close species pair consists of any given species, together with that other from which it is most difficult to separate morphologically. From a biological viewpoint, we shall be concerned with questions relating to whether or not such segregates do represent species isolates, or whether they may simply reflect some disjunct aspect of infraspecific variation. In *Ophion*, there are several close species pairs within which statistical analysis is very desirable for a logical, objective answer to be made to such questions. The actual analysis proceeds along several inter-related lines of inquiry:

(1) Statistical aspects of morphological isolation. Where statistical rather than absolute differences exist between members of a close species pair, some form of comparison of character state frequency distributions is obviously desirable. Two points must be made here: (a) where sexual dimorphism or any other factor affects the shape of the distributions, a non-parametric test should replace the usual parametric equivalent for significance testing; (b) assignation of identity to specimens used for investigating suspect bimodality in continuous variables *must* be based entirely upon characters other than that being analysed (otherwise, an element of circular reasoning will enter into our species concept!).

I have adopted the Mann-Whitney test in place of the more familiar "t" test for comparison of frequency distributions. Such distributions rarely seem to follow a near-normal form. For the most part, I have been concerned with comparison of the number of flagellar segments between members of a close species pair, since this character possesses a large variance, which is also easily compartmentalised on a direct numerical scale. Specimens from which these data were drawn had previously been identified on characters other than flagellar segment number.

An expected result for isolating members of a close species pair would be based on significant bimodality of two approximately symmetrical distributions for number of flagellar segments. Areas of actual overlap would be biologically acceptable, owing to the fact that initial species diagnosis was not based upon that same character.

(2) Behavioural criteria. There are two very important aspects of behaviour which bear directly on the question of species identity: (a) the *temporal frequency distribution* (based upon dates of capture for as large a sample as possible); (b) *host preference*. Expected correlations for true species isolates would be based on the hypothesis that closely related species would be likely to exhibit behavioural divergence in these two niche-related parameters. In parasites, it might be expected that selected hosts appear at different seasons for two related parasite species — or that two synchronously appearing parasites avoid competition by modifying their host preferences. Where two morphologically distinct species appear at the same time, attacking the same hosts, we may have reason to suspect that these are not biologically distinct units.

Areas of difficulty.

There are several complicating factors which render the foregoing criteria less than perfect in reality. Dimorphism (and polymorphism) may occur not only in relation to obvious sexual differences, but also in correlation with environmental factors. Where the host range of a species contains a disjunct size distribution, the parasite may also exhibit disjunct variation. Environmental influences acting upon species with an extended flight period may also be reflected in morphological variation in parasites. Mem-

bers of a close species pair could therefore be forms of a single species which has been subjected to differing environmental influences surrounding embryogenesis.

In attempting to find a solution to one problem of the kind just mentioned, I have looked for evidence arising from the regression of flagellar segment number on wing length. This is a special rather than general technique, which is explained in detail at a later point.

A further problem lies in the possibility that biologically distinct species need not exhibit morphological differences. It is possible that certain bivoltine parasite species really represent two biologically isolated forms, each with a complete annual life cycle. This will come to light only when (for example) "spring brood" parasite larvae produce adults the following spring instead of appearing at the normal "second brood" time. However, this could also be interpreted as a single parasite species with different developmental periods dependent upon host size or upon other environmental factors. This is a real, rather than imaginary problem with certain *Ophion* species. Hopeful solutions to these difficulties are presented following formal description of the species concerned. In one case, a small scale behavioural experiment was conducted in order to support the interpretation of other sources. The relative scarcity of rearing records and utter lack of breeding experiments with *Ophion* obviously contribute greatly to some of the major problems discussed herein.

Generic Diagnosis

The genus *Ophion* can be recognised by the recent keys of Townes (1971), also Gauld (1973). Gauld also discusses recognition of *Platophion* as a genus distinct from *Ophion*, the former segregate not having been recognised by Townes (loc. cit.). Most of the characters given by Gauld for separation of *Platophion* may occur in *Ophion* s. str., but there still remains some evidence to suggest that these genera are best retained as separate entities (see also Oosterbroek, 1978). The genus *Platophion* is not treated in the present study. I have appended short notes on species discrimination in *Platophion* (Appendix).

Key to the species

1. Small species (wing length at most 11 mm); nervellus distinctly reclivous above (fig. 3); body frequently yellow marked (cf. fig. 6b), never black patterned; flagellum with 40— 49 segments; propodeum with reduced carination, at least in region anterior to the posterior transverse carina (cf. fig. 5); radius somewhat thickened towards junction with stigma (fig. 4); clypeus up to more than twice wider than high. (Widely distributed, often common)...... *minutus* Kr.
— Wing length usually over 11 mm, nervellus rarely distinctly reclivous, excepting when body distinctly black patterned, or when there are less than 50 flagellar segments; propodeum rarely lacking carinae anterior to posterior transcarina (cf. figs. 15, 50); radius not, or scarcely thickened towards stigma (fig. 38); clypeus usually much less than twice wider than high 2
2. Body with distinctive black pattern (cf. fig. 6a); thorax with large punctures; wings orange tinted; nervellus tending to be reclivous above, radius slightly thickened towards stigma. (Widely distributed, seldom common) .... *ventricosus* Grav.
— Head and thorax not black marked; thorax with superficial puncturation; wings generally hyaline; nervellus rarely reclivous above, radius not noticeably thickened towards stigma........................ 3
3. Antennal flagellum rarely with less than 64 segments; hind femur very slender (cf. fig. 30a), hind coxae elongate — appearing smaller to slightly larger in area than the lateral area of the propodeum, latter often with no keel connecting the carina lateralis to the spiracle (fig. 8); mid tibial spurs of nearly equal length; punctures of epistoma tending to be further apart than those of facial orbits (fig. 9); ocellar-ocular interspace from almost absent in females to 0.65 × interocellar space in some males, diameter of hind ocellus often as much as twice distance between ocellus and occipital carina; mesonotum often dark suffused. (Common species of early spring) .... *scutellaris* Ths.
— Flagellum usually with less than 64 segments; hind femur less slender (figs. 30b-d); hind coxae slightly to very much larger in area than the lateral area of the propodeum, carina lateralis generally connected to spiracle by a keel (fig. 43); mid tibial spurs usually of very unequal length; punctures of epistoma often as close or even closer together than those of orbits (e.g. fig. 21); ocelli various, hind ocelli frequently smaller in relation to distance to occipital carina; mesonotum only dark suffused
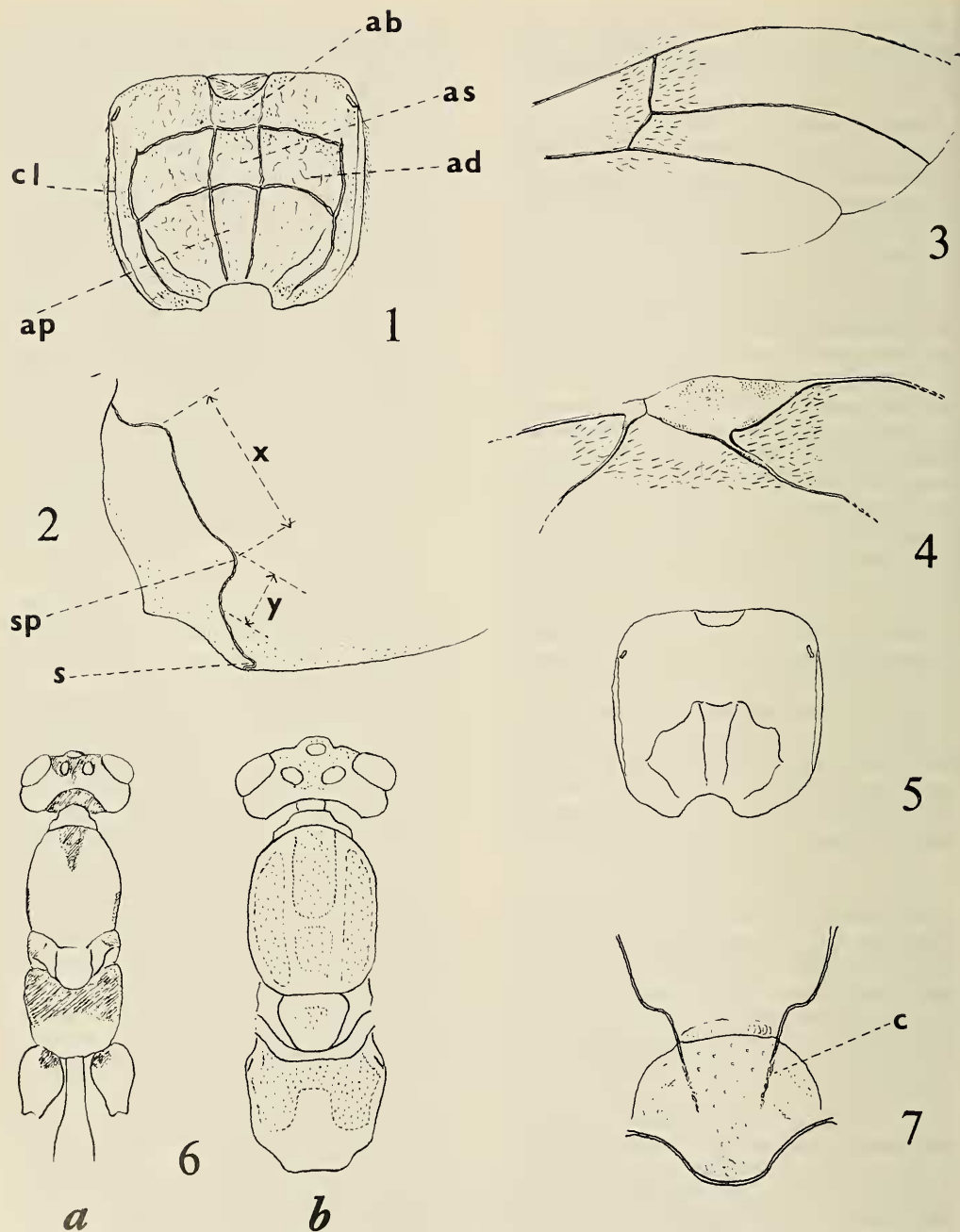
Fig. 1. Propodeum, dorsal (generalised), showing terminology of carinae and areae: *cl*, carina lateralis; *ap*, area petiolaris; *ab*, area basalis; *as*, area superomedia; *ad*, area dentiparis. Fig. 2. Mesosternopleuron, antero-lateral, showing terminology of the epicnemial carina. *sp*, sternopleural angle; *s*, sternal angle; *x*, upper sector; *y*, lower sector. Fig. 3—5. *Ophion minutus* Kriechbaumer; 3, nervellus of hind wing; 4, fore-wing — stigma and base of radius; 5, propodeum, dorsal (maximum development of dorsal carinae). Fig. 6. Head, thorax and propodeum, showing patterning in: (a) *Ophion ventricosus* Gravenhorst, (b) *O. obscuratus* Fabricius. Fig. 7. *Ophion scutellaris* Thomson, lateral carinae (c) of mesoscutellum.

when yellow markings are also present (fig. 6b) 4

4. Males 5
— Females 6

5. Ocellar-ocular interspace *at least* wider than the posterior sulcus of the stemmaticum (fig. 33) — *very often in range* 0.25 to 1.0 × *interocellar space* (see figs. 11, 18, 23); posterior sulcus of stemmaticum most usually joining lateral sulcus without first touching compound eye, although it may connect to latter by means of a stemmatico-ocular line (fig. 28), especially when the ocellar-ocular interspace is long 7
— Posterior ocelli actually touching eyes (figs. 47, 51), or separated from them by width of the posterior sulcus of the stemmaticum only — in which case the latter touches the compound eye, often without connecting to the lateral sulcus (which may be weak or absent) (fig. 40); stemmatico —ocular line rarely in evidence 22

6. Ocellar-ocular interspace wider than posterior sulcus of stemmaticum, (fig. 33), *very often in range* 0.2 to around 0.5 × *interocellar space* (figs. 11, 20, 23); posterior sulcus of stemmaticum very often connecting with lateral sulcus — whether or not former joins compound eye (cf. fig. 33) 7
— Posterior ocellus touching compound eyes, or separated from them only by the width of the posterior sulcus of the stemmaticum — latter often running into back of eye without connecting to lateral sulcus of stemmaticum, which latter may be weak or absent (figs. 40, 47, 51) 22

7. Ocellar-ocular interspace often more than 0.25 × interocellar space (figs. 11, 20, 25); vertex generally weakly to sharply angled centrally (figs. 20, 23, 47, 51) and/or hind trochantellus greater or equal in length to its minimum width in dorsal view (e.g., fig. 10a); body often yellow patterned (cf. fig. 6b); carina lateralis of propodeum often weaker than the dorsal carinae or even absent (fig. 16). — Mandible often with distinct puncturing on ventral flange, frequently in combination with acute gape and weak internal angles to teeth (fig. 14); radius usually sinuate towards base (fig. 38a); scutellum rarely carinate when first flagellar segment is much more than 3.0 × longer than broad 8
— Ocellar-ocular interspace never greater than about 0.25 × interocellar space; occip-

ital carina usually squared, dipped or rounded centrally on vertex (figs. 11, 33, 40) and/or hind trochantellus shorter than its minimum width in dorsal view (fig. 10b); body rarely yellow patterned above; carina lateralis more usually about as strong as the other dorsal carinae (fig. 43). — Mandible with at most a few fine punctures on ventral flange, the gape obtuse to rectangular, internal angles to teeth sharply defined (fig. 37); radius quite often evenly curved towards base (fig. 38b); one species frequently has the scutellum carinate (fig. 7), *and* the first flagellar segment well over 3.0 × longer than broad 22

8. Body without yellow patterning, stigma not yellow at *apex* 9
— Body yellow patterned (cf. fig. 6b) — or stigma with conspicuous yellow apex ... 14

9. Males 10
— Females 11

10. *Head less buccate* — i.e. agreeing with *at least* two of the following: ocellar-ocular interspace less than 0.4 × interocellar space; distance between posterior ocellus and occipital carina less than 0.8 × diameter of a posterior ocellus and less than 2.0 × maximum width of first flagellar segment (dorsal head characters, figs. 11a, 19, 23); gena less than 0.45 × width of base of mandible (figs. 9, 12, 21). — Flagellum with at least 51 segments, temple always shorter than eye length (cf. fig. 11a) 14
— *Head more buccate* — ocellar-ocular interspace *at least* 0.4 × interocellar space; distance between posterior ocellus and occipital carina *at least* 0.8 × diameter of ocellus, usually not less than 2.0 × maximum width of first flagellar segment (except when latter is only around 3.0 × longer than broad) (figs. 11b, 25, 28); gena *at least* 0.45 × width of base of mandible (figs. 13, 26, 29). — Flagellum often with less than 51 segments, temple about as long or even longer than eye (figs. 25, 27, 28)............. 12

11. *Head less buccate* — i.e., ocellar-ocular interspace usually much less than 0.4 × interocellar space, distance between posterior ocellus and occipital carina usually less than 0.8 × diameter of a posterior ocellus and up to c. 1.3 × maximum width of first flagellar segment (fig. 11a); gena *at most* 0.4 × width of mandible base (figs. 9, 12, 21). — Flagellum with at least 51 segments. Temple always distinctly shorter than eye
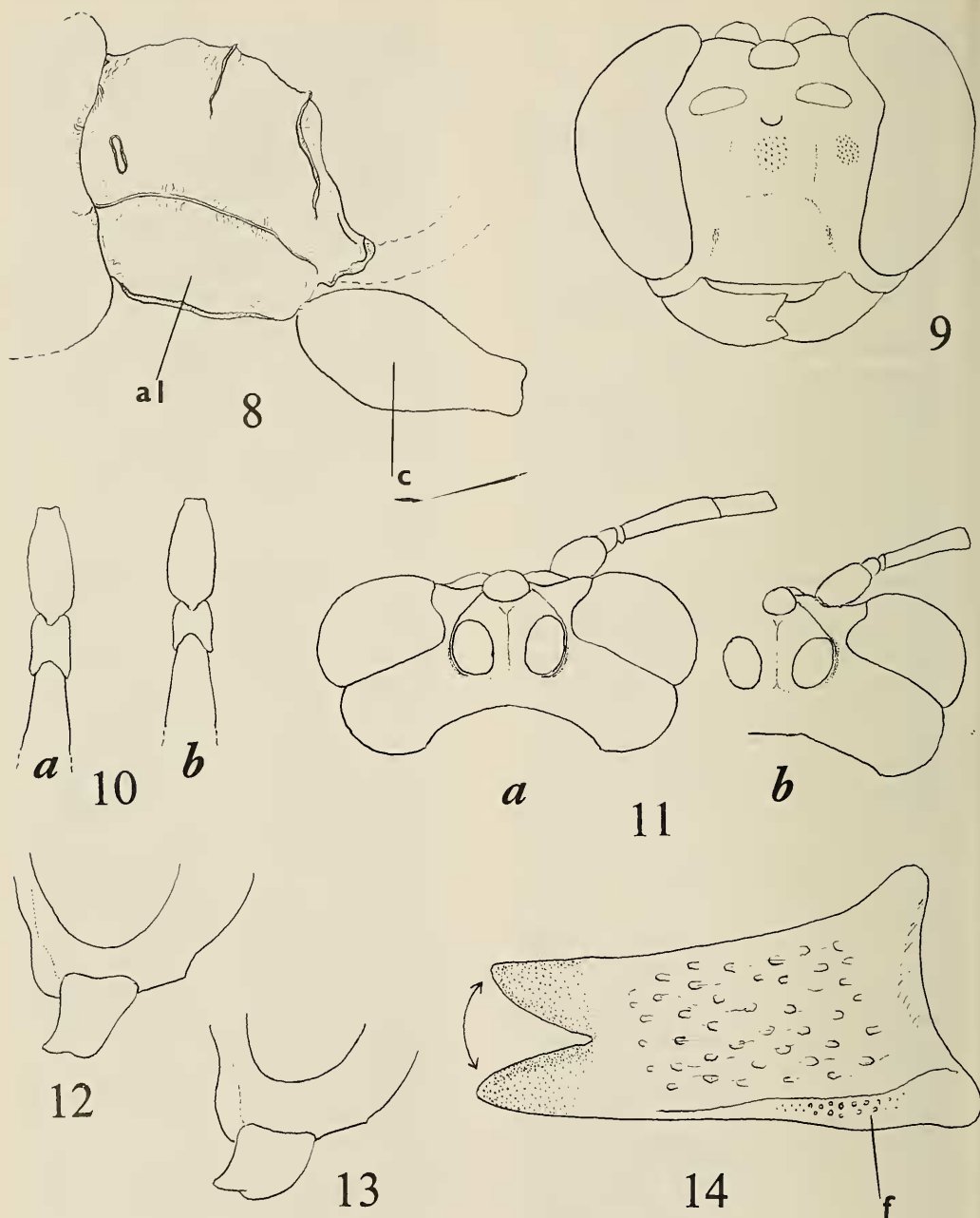
Figs. 8, 9. *Ophion scutellaris* Thomson; 8, propodeum, lateral, *al* = lateral area, *c* = hind coxa; 9, head, frontal view. Fig. 10. Hind trochantelli, a) elongate form, b) short condition. Figs. 11—14. *Ophion luteus* (Linnaeus); 11, heads, dorsal, (a) and indicating range of variation (b); 12, head, lateral; 13, ditto — showing longer genal condition; 14, mandible, mandibular gape indicated by arrow, *f* = mandibular flange.

(fig. 11a) 14

— *Head more buccate* — i.e., ocellar-ocular interspace *at least* 0.4 × interocellar space, distance between posterior ocellus and occipital carina *at least* 0.8 × ocellar diameter and greater than or equal to 1.3 × maximum width of first flagellar segment (except when latter is only around 3.0 × longer than broad) (figs. 27, 28); gena 0.35 to 0.65 × width of base of mandible (figs. 12,29). — Flagellum often with less than 51 segments. Temple up to as long as eye (fig. 27) 12

12. Occipital carina rounded, squared or dipped centrally (sometimes weakly angled) (figs. 11, 33, 40); hind trochantellus as long or longer than its minimum width in dorsal view (fig. 10a); mandible usually with an acute gape, weak internal angles to the teeth, the flange distinctly punctate medially (fig. 14) 14

— Occipital carina weakly to sharply angled centrally figs. 19, 20); hind trochantellus often shorter than its minimum width in dorsal view (fig. 10b); mandible with a rectangular or obtuse gape, sharp internal angles and more or less impunctate flange (fig. 37) 13

13. Temple shorter than eye length; flagellum with at least 51 segments; stigma usually yellow at *apex* when flagellum has less than 57 segments; hind trochantellus more usually as long as its minimum width in dorsal view (fig. 10a) 16

— Temple at least equal to eye length, and/or flagellum with less than 51 segments; stigma never yellow at apex; hind trochantellus always shorter than its minimum width in dorsal view (fig. 10b) 17

14. Occipital carina usually rounded, squared or dipped centrally, sometimes weakly angled (fig. 11, 33, 40); mandibular gape usually acute, with weak (or no) internal angles at base of teeth (fig. 14); epistomal punctures often similar to or of *sparser* distribution than those of facial orbits; lateral carina of propodeum generally absent or more weakly defined than the dorsal carinae (fig. 16, also 50); mesopleura with weakly sculptured interspaces between the punctures. — First flagellar segment often distinctly greater than 4.0 × longer than broad (fig. 11); postgena greater than or equal to length of genal inflection (cf. figs. 12, 13); stigma rarely paler at apex, body

rarely yellow patterned. Extremely variable, especially in genal length, interocellar space and other head characters (Abundant) .... *luteus* L.

— Occipital carina weakly to very sharp-angled centrally (figs. 20, 23, see also 47, 51); mandibular gape obtuse to rectangular, internal angles of teeth sharp (fig. 37); punctures of epistoma similar to, or of *closer* distribution than those of orbits (fig. 21); lateral carina of propodeum sometimes complete and strong; mesopleural interspaces more roughly sculptured on average. Hind trochantellus sometimes much shorter than minimum width (fig. 10b). — First flagellar segment less than 3.0 to around 4.0 × longer than broad (sometimes a little longer) (figs. 19, 20, 23); postgena usually in range of *less than*, or equal to length of genal inflection; stigma often yellow at apex *(typically* in combination with yellow patterned body, fig. 6b) 15

15. Flagellum with less than 50 segments; distance between posterior ocellus and occipital carina around 2.0 or more × maximum width of first flagellar segment (fig. 18); third abdominal tergite not more than twice as broad apically as at base, in lateral view (fig. 17a); the central flagellar segments tending to be less elongate on average; Mesonotum "vittate" (fig. 6b). (Rare, sand dunes) .... *forticornis* Mrly.

— Flagellum with at least 51 segments (usually more); distance between posterior ocellus and occipital carina much less than 2.0 × maximum width of first flagellar segment (figs. 19, 23); third tergite up to 3.0 × wider at apex than at base (fig. 17b); central flagellar segments tending to be more elongate in yellow marked examples 16

16. Body usually richly yellow patterned (fig. 6b), stigma rarely lacking yellow apex when other markings are absent; first flagellar segment usually over 3.0 × longer than broad when there are 57 or more flagellar segments (fig. 19); sternopleural angle of epicnemium obtuse to (sometimes) weakly acute (fig. 22); hind trochantellus generally about as long as its minimum width in dorsal view (cf. fig. 10a); general microsculpture finer (see fig. 22); hind femur more slender on average (figs. 30a/b, sometimes c); scutellum not carinate laterally; propodeum sometimes with area basalis, but rarely with area dentipara or closed superome-
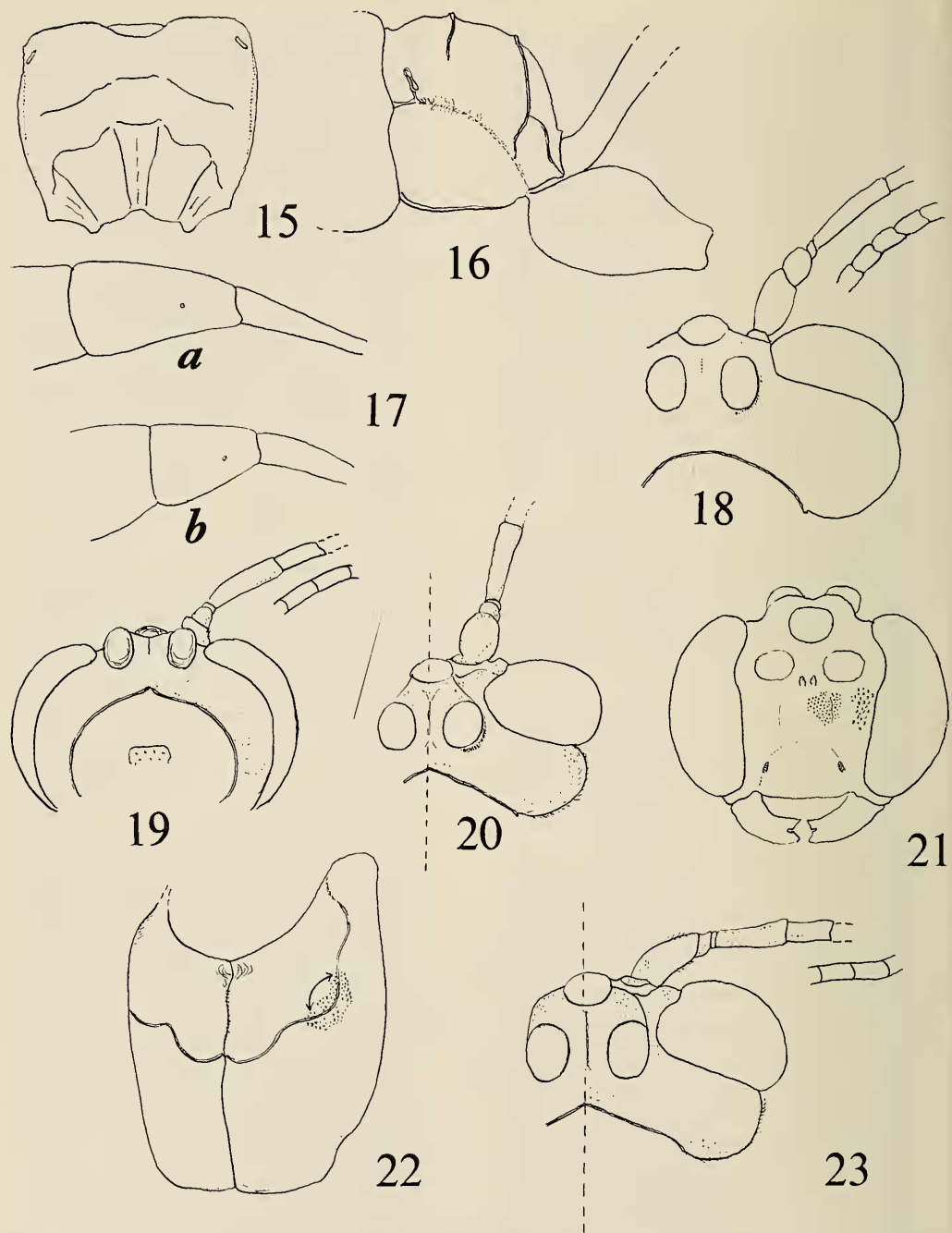
Figs. 15—16. *Ophion luteus* (Linnaeus); 15, propodeum, dorsal; 16, propodeum, lateral. Fig. 17. (a) *Ophion forticornis* Morley, abdominal tergites 1—3, lateral; (b) *Ophion obscuratus* Fabricius, the same. Fig. 18. *Ophion forticornis* Morley, head, dorsal (central flagellar segments inset). Figs. 19—22. *Ophion obscuratus* Fabricius; 19, head, postero-dorsal view (central flagellar segments inset); 20, head, dorsal; 21, head, frontal view; 22, mesothorax, slightly rotated ventral view — sternopleural angle of epicnemium arrowed. Fig. 23. *Ophion crassicornis* sp. nov., head, dorsal (central flagellar segments inset).
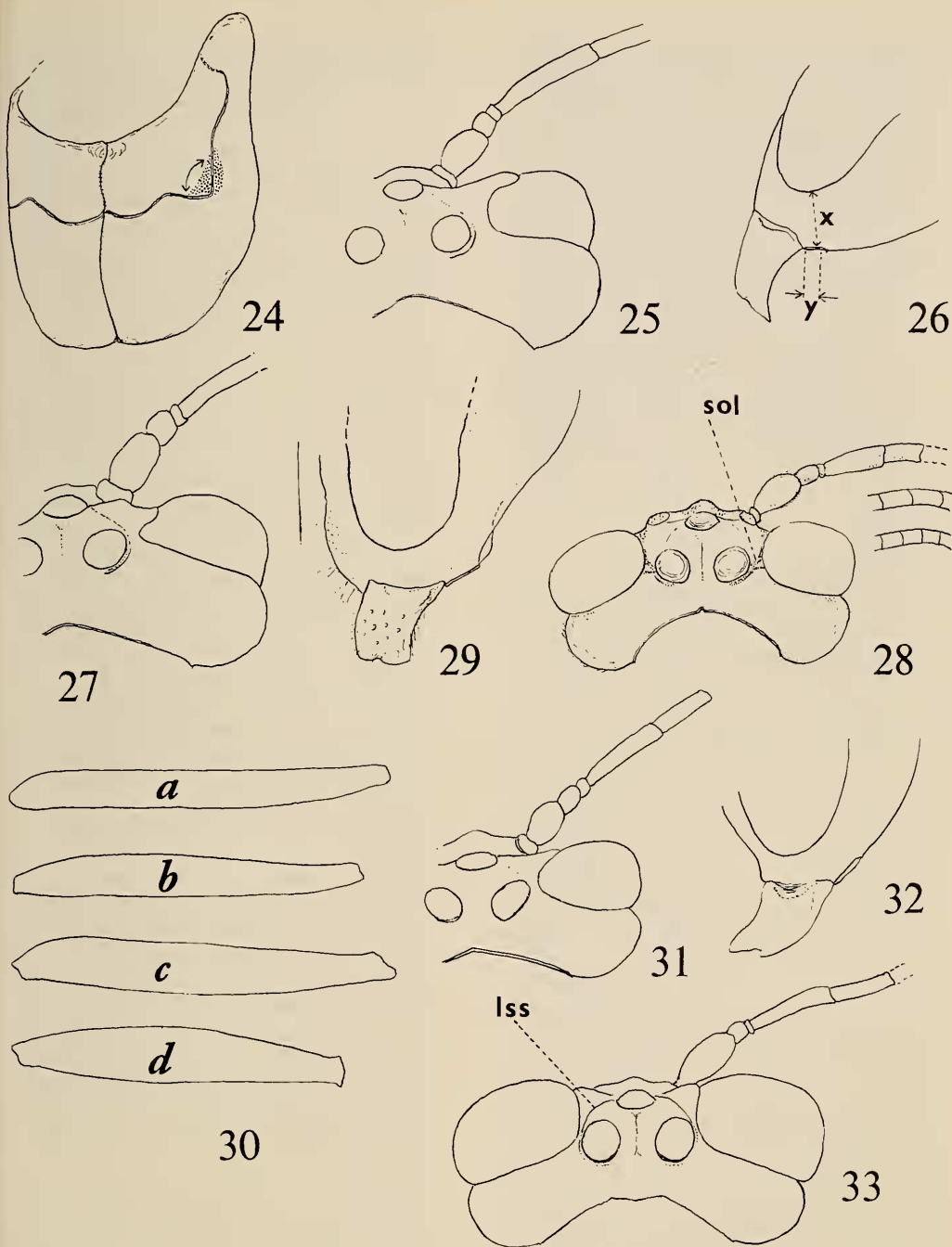
Fig. 24. *Ophion crassicornis* sp. nov., mesothorax, slightly rotated ventral view — sternopleural angle of epicnemium arrowed. Fig. 25—27. *Ophion longigena* Thomson; 25, head, dorsal (male); 26, head, lateral — *x*, postgenal length, *y*, length of genal inflection; 27, head, dorsal (female). Figs. 28—29. *Ophion brevicornis* Morley; 28, head, dorsal (female) (proximal and central, flagellar segments inset), *sol*, stemmatico-ocular line; 29, head, lateral (female). Fig. 30. Range of form of hind femur in *Ophion* species. Figs. 31—32. *Ophion perkinsi* sp. nov.; 31, head, dorsal; 32, head, lateral. Fig. 33. *Ophion pteridis* Kriechbaumer, head, dorsal — lss = lateral sulcus of stemmaticum.

dia (see fig. 1). Polymorphic. (Abundant, March to January, with peaks in spring and autumn) .... *obscuratus* F.
— Body not yellow patterned, stigma lacking pale apex; first flagellar segment from less than 3.0, to (sometimes) 4.0 × longer than broad (fig. 23); flagellum with at least 57 segments; sternopleural angle of epicnemium usually sharply acute angled (fig. 24); hind trochantellus often distinctly shorter than its minimum width in dorsal view (approaching fig. 10b); general microsculpture rougher (see fig. 24); hind femur thicker on average (figs. 30c, sometimes b); scutellum often with lateral carinae (fig. 7); propodeum lacking area basalis, but often with dentiparal carinae *and* closed area superomedia. (Uncommon, early to mid-summer) .... *crassicornis* sp. nov.
17. Males 18
— Females 20
18. Temple around 1.3 × eye length, very strongly expanded behind eyes in dorsal view; ocellar-ocular interspace over 0.5, to about 1.0 × interocellar space; distance between posterior ocellus and occipital carina 2.5 — 3.0 × maximum thickness of first flagellar segment (latter about 4.0 × longer than broad) and 0.8 to 2.0 × diameter of a posterior ocellus (head, dorsal fig. 25); postgena around 4.0, to nearly 6.0 × length of genal inflection, latter distinctly less than 0.4 × width of mandible base; gena 0.8 to 1.0 × base of mandible (head, lateral fig. 26); eyes strongly divergent beneath in frontal view; flagellum with 48 to 56 segments (small sample). (Very rare, perhaps southern; early summer) .... *longigena* Ths.
— Temple not or scarcely longer than eye, less expanded behind; ocellar-ocular interspace not greater than 0.8 × interocellar space; distance between posterior ocellus and occipital carina not greater than 2.0 × maximum thickness of first flagellar segment (latter sometimes only around 3.0 × longer than broad) and at most 1.7 × diameter of posterior ocellus (heads, dorsal figs. 28, 31); postgena not more than 2.0 × length of genal inflection; latter not less than 0.4 × width of mandible base; gena often less than 0.8 × latter dimension (heads, lateral figs. 29, 32); eyes at most slightly divergent; flagellum most often with less than 50 segments 19

19. Petiolar membrane approximately opposite line of spiracles (cf. fig. 43); first flagellar segment up to 3.4 × longer than broad or less; temple about equal to eye length and up to 1.5 × length of first segment of flagellum (fig. 28); scutellum at most weakly carinate. (Rare) .... *brevicornis* Morl.
— Petiolar membrane far behind line of spiracles (cf. fig. 35); first flagellar segment around 4.0, to about 5.0 × longer than broad; temple at most a little longer than first segment of flagellum (fig. 31); scutellum generally with strong lateral carinae (cf. fig. 7). (Rare, but widespread in Britain) .... *perkinsi* sp. nov.
20. Temple fully as long as eye; distance between posterior ocellus and occipital carina up to 1.6 × diameter of a posterior ocellus (fig. 25); genal inflection less than 0.45 × width of mandible base; postgena at least around 4.0 × length of genal inflection (fig. 26); abdomen sometimes broadly black across apex; flagellum with 48 to 56 segments (small sample!). Rare, perhaps southern .... *longigena* Ths.
— Temple not quite as long as eye; posterior ocellus to occipital carina up to 1.3 × ocellar diameter (figs. 28, 31); genal inflection not less than 0.45 × width of base of mandible; postgena less than 2.0 × genal inflection (fig. 32); abdomen sometimes darkened ventrally, but not determinately black apically; flagellum usually with less than 50 segments 21
21. Petiolar membrane approximately in line with the spiracles (cf. fig. 43); first flagellar segment up to about 3.4 × longer than broad; temple slightly shorter than eye and up to 1.5 × length of first flagellar segment: distance between posterior ocellus and occipital carina *at most* 1.8 × maximum width of first flagellar segment; central flagellar segments subquadrate, the antenna unusually short and thick (head, dorsal, fig. 28); gena greater than or equal to 0.5 × width of base of mandible. (Rare) .... *brevicornis* Morl.
— Petiolar membrane emitted well behind line of spiracles (cf. fig. 35); first flagellar segment in region of 4.0 to 5.0 × longer than broad; temple much shorter than eye and about same length as first flagellar segment, or a little longer; distance between posterior ocellus and occipital carina 1.5 to 2.0 × maximum width of first flagellar segment;

central flagellar segments elongate, the antenna more slender in appearance (head, dorsal, fig. 31); gena less than or equal to 0.5 × width of mandible base (fig. 32). (Rare, but widespread in Britain) . . . .
. . . . *perkinsi* sp. nov.

22. Mandible more elongate on average, usually with a distinctly punctate flange, often with an acute gape combined with weak or absent internal angles to the teeth (fig. 14); hind trochantellus usually at least as long as its minimum width in dorsal view (fig. 10a), sometimes shorter; carina lateralis of propodeum tending to be absent or weaker than the more dorsal carinae (fig. 16) when vertex is not angled at the occipital carina (e.g. figs. 11, 33, 40); body very often yellow patterned (fig. 6b) including *apex* of stigma; scutellum rarely carinate (excepting when the first flagellar segment is only around 3.0 × longer than broad); radius always sinuate towards base (cf. fig. 38a) 14

— Mandible shorter and wider on average, the flange with at most a few minute punctures medially, the gape rectangular to obtuse, internal angles of teeth sharply defined (fig. 37); hind trochantellus always shorter than its minimum width in dorsal view (fig. 10 b); carina lateralis usually about as strong as the dorsal propodeal carinae when vertex not angled centrally on occipital carina (fig. 43); body (including stigmal apex) rarely with distinctive yellow patterning; scutellum often carinate (fig. 7), in which case first flagellar segment much more elongate (e.g. figs. 34, 40); radius quite often not or scarcely sinuate towards base (fig. 38b) 23

23. First flagellar segment usually *at least* 3.4 × as long as broad (figs. 33, 40); carina lateralis usually about as strong as the dorsal propodeal carinae (fig. 43); pleurosternal angles of epicnemium far anterior to sternal angles, excepting when former are very obtuse angled (figs. 36, 42); substigmal speculum more or less extending beneath the prestigma (fig. 39) *or* trichiae in this region much longer than width of adjacent crossvein (fig. 34); top edge of mandible basally narrower than width of a tooth (fig. 45) — except when the edge is rounded into front of mandible. — Scutellum often carinate (fig. 7); radius often not sinuate towards base (fig. 38b). 24

— First flagellar segment often less than 3.0 × longer than broad, rarely more than 3.3 ×

(figs. 47, 51); carina lateralis very often absent or weaker than the dorsal propodeal carinae (fig. 50); pleurosternal angles of epicnemium very often nearly in line with sternal angles, not broadly obtuse, often sharp (figs. 49, 52); substigmal speculum not extending beneath prestigma, the trichiae in this region at most marginally longer than the adjacent crossvein is wide (fig. 48); top edge of mandible basally about same width as a tooth, edge sharply defined from front of mandible (fig. 46). Scutellum rarely with trace of carinae; radius always sinuate towards base (cf. fig. 38a) 25

24. Scutellum often carinate (fig. 7); radius sinuate towards base of second abscissa (fig. 38a); membrane of petiolar segment well behind line of spiracles (fig. 35); number of flagellar segments rarely less than value of: 1.19 × wing length (mm) + 36.45 (to nearest whole number); pleurosternal angles of epicnemium rectilinear to somewhat obtuse, lower sector of epicnemium usually not more than about 0.5 × upper sector (fig. 36); lateral sulci of stemmaticum about as deep, or deeper than the middorsal sulcus (fig. 33). — Colour more reddish, microsculpture coarser; area superomedia usually open posteriorly and petiolar carinae less complete (cf. fig. 15); facioclypeal area more quadrate on average. (Common and widespread) . . . . *pteridis* Kr.

— Scutellum rarely with trace of carinae; radius often evenly curved towards base of second abscissa (fig. 38b); membrane of petiolar segment approximately opposite the spiracles (fig. 43); number of flagellar segments rarely more than value of: 1.13 × wing length (mm) + 37.5 (nearest whole number); pleurosternal angles of epicnemium usually rounded and broadly obtuse, lower sector of pleural epicnemium generally nearer 0.6 × upper sector (fig. 42); lateral sulcus of stemmaticum usually weaker than middorsal sulcus, frequently obsolete or absent (fig. 40). Colour more testaceous, frequently with yellow markings (sometimes as in fig. 6b); microsculpture weak; area superomedia more often closed, petiolar carinae more complete (cf. fig. 1); facioclypeal area more transverse on average. (Common, apparently less so Northwards) . . . . *parvulus* Kr.

25. Flagellum with 50-58 segments; nervellus broken at, or below centre; occipital carina
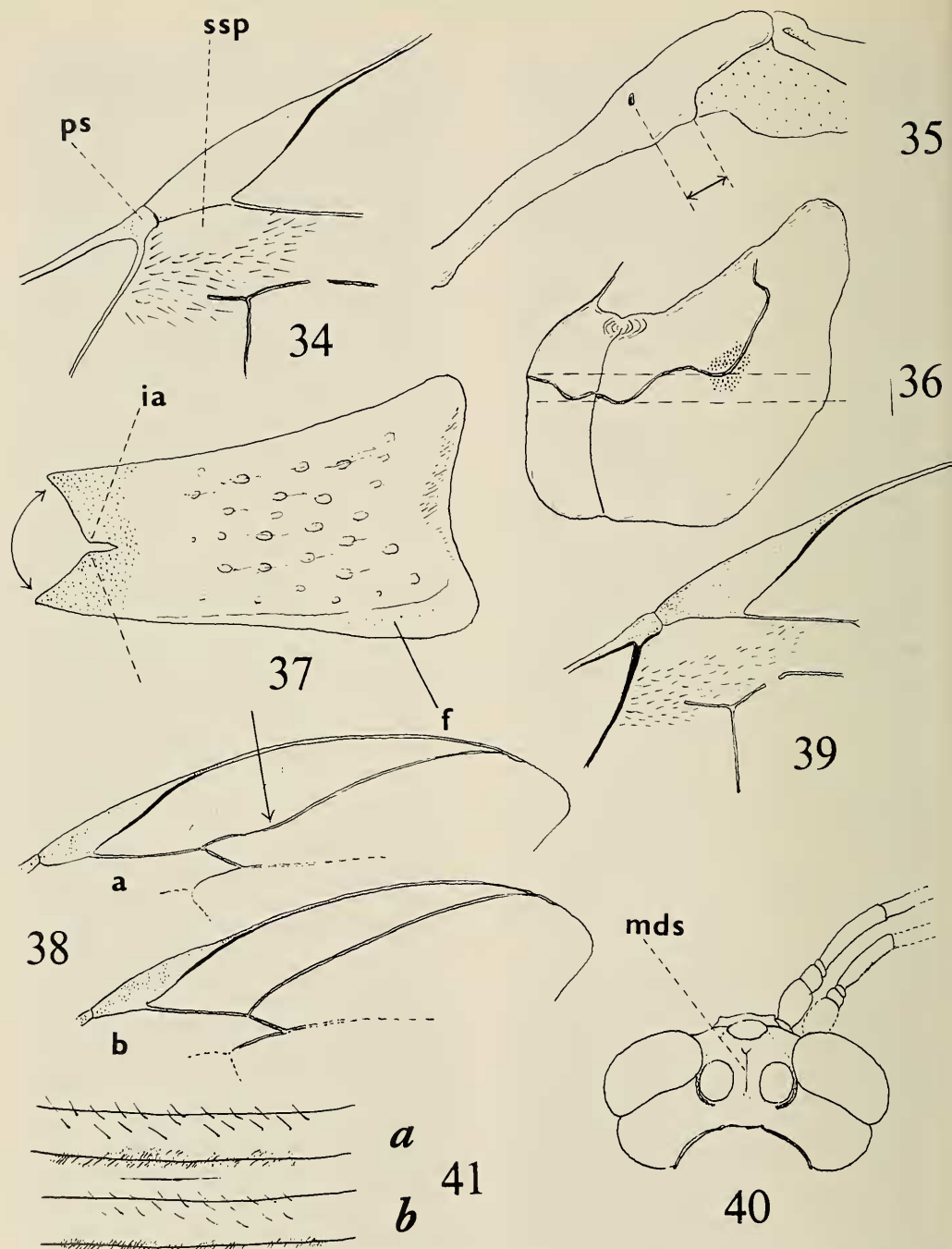
Figs. 34—37. *Ophion pteridis* Kriechbaumer; 34, fore wing, trichiation of disco-cubital cell — *ps* = prestigma, *ssp* = substigmal speculum; 35, first abdominal segment, lateral (relative positions of spiracle and sternal membrane indicated); 36, mesothorax, slightly rotated ventral view — broken lines indicating degree of opposition of epicnemial angulations; 37, mandible, frontal view — gape arrowed, *ia* = internal angle of tooth, *f* = flange. Fig. 38. Fore wing, stigma and radius; (a) *Ophion pteridis* Kriechbaumer, (b) *Ophion parvulus* Kriechbaumer. Radial sinuation arrowed in (a). Figs. 39—40. *Ophion parvulus* Kriechbaumer; 39, fore wing, trichiation of disco-cubital cell; 40, head, dorsal (variation in shape of first flagellar segment indicated, inset), *mds* = mid-dorsal sulcus. Fig. 41. Hind tibiae, central region, showing spinulation, in (a) *Ophion luteus* (Linnaeus) and (b) *Ophion parvulus* Kriechbaumer.
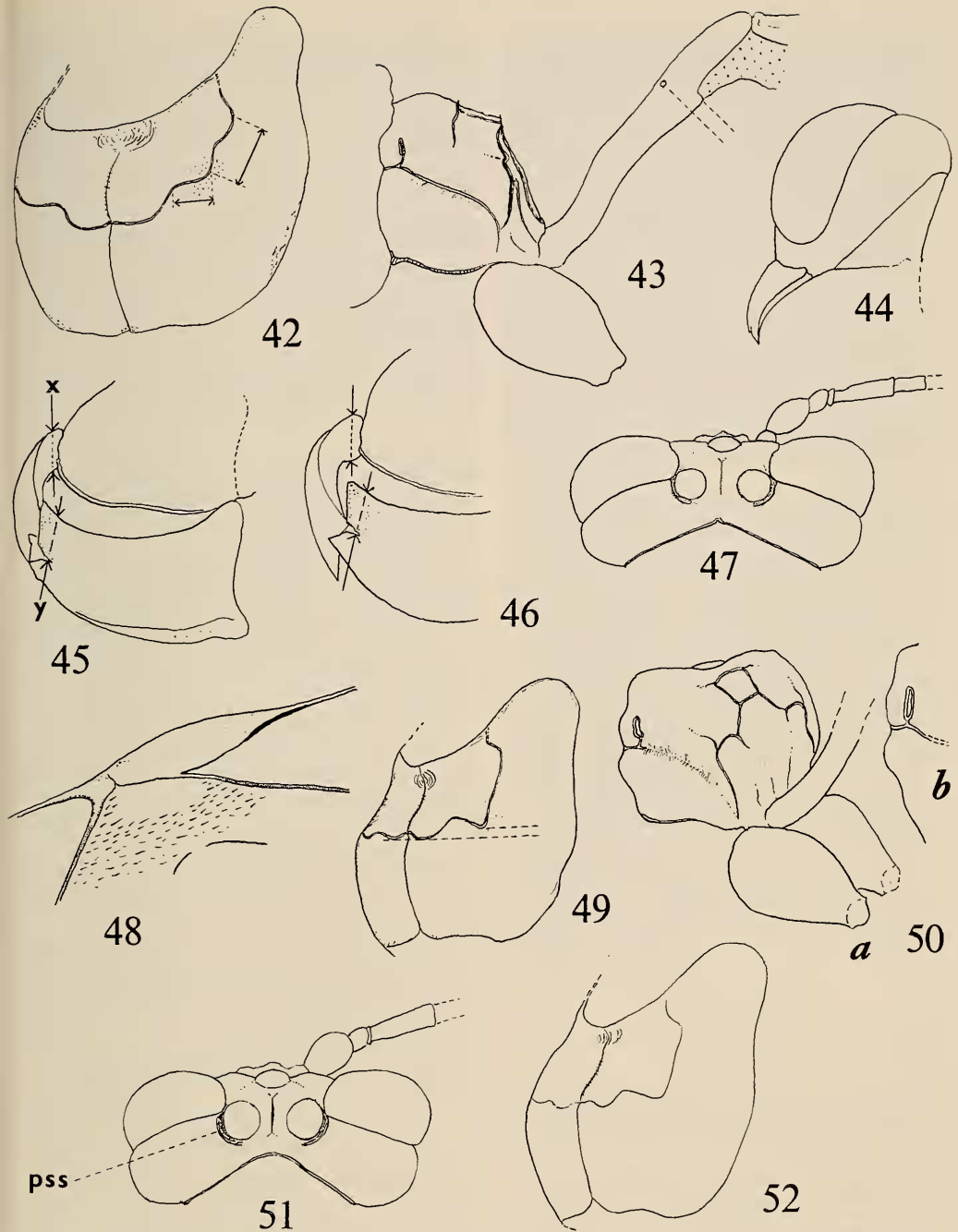
Figs. 42—45. *Ophion parvulus* Kriechbaumer; 42, mesothorax, slightly rotated ventral view, lengths of lower and upper sectors of epicnemial carina arrowed; 43, propodeum and first gastral tergite, lateral. Juxta-position of spiracle and sternal membrane indicated; 44, head, sub-ventral view of left half, showing relative lengths of genal inflection and postgena; 45, mandibles, lateral view — x = basal width of top edge, y = (maximum) width of (dorsal) tooth. Fig. 46—50. *Ophion mocsaryi* Brauns; 46, mandibles, lateral view; 47, head, dorsal; 48, trichiation of disco-cubital cell; 49, mesothorax, rotated ventral view, opposition of epicnemial angles indicated; 50, propodeum and hind coxa, sinistro-posterior view, (a), spiracular shape, (b) (inset), ditto in *O. costatus* Ratzeburg. Figs. 51—52. *Ophion costatus* Ratzeburg; 51, head, dorsal — *pss* = posterior sulcus of stemmaticum; 52, mesothorax, rotated, ventral view.

more angled centrally, distance between posterior ocellus and occipital carina usually greater (never less) than maximum width of first flagellar segment and usually around 0.7 × ocellar diameter; ocellar interspace often wider than maximum width of first flagellar segment, the latter 2.4 to about 3.5 × longer than broad; posterior sulcus of stemmaticum moderately impressed (head, dorsal fig. 47); lower sector of pleural epicnemium usually less than 0.6 × length of upper sector (fig. 49); propodeum usually nearly completely areolated, but with the carina lateralis absent to weaker than dorsal carinae in most specimens; propodeal spiracle more ovoid (fig. 50a); last two segments of maxillary palpus moderately to strongly unequal in length. (Widespread, sometimes common) . . . . *mocsaryi* Brauns

— Flagellum with 56-63 segments; nervellus frequently broken *above* centre; occipital carina rounded to weakly angled; posterior ocellus to occipital carina usually less, seldom greater than width of first flagellar segment and usually less than 0.7 × ocellar diameter; ocellar interspace often narrower than first flagellar segment, latter shorter on average (often much less than 3.0 × longer than broad); posterior sulcus of stemmaticum very deeply impressed (head, dorsal fig. 51); lower sector of epicnemium usually nearer 0.6 × upper sector (fig. 52); propodeum with or without a strong carina lateralis (cf. figs. 1 & 43); propodeal spiracle more linear (fig. 50b); last two segments of maxillary palpus equal, to moderately unequal in length. (Widespread, seldom common) . . . . *costatus* Ratzburg

SYSTEMATIC PART

Ophion
Fabricius

Ophion Fabricius, 1798, Entomologica Systematica, suppl.: 210, 235. Species: Type *Ichneumon luteus* Linnaeus, designated by Curtis, 1835.

Ophion minutus Kriechbaumer
(figs. 3—5)

Ophion minutus Kriechbaumer, 1879: 105 (lectotype male, Munich). Schmiedeknecht, 1908. Morley, 1915. Perkins, 19-- (MS). Townes et al., 1965 (in part). Gauld, 1973, 1976, 1978. Oosterbroek, 1978.
Ophion parvulus Kriechbaumer; Morley, 1915 (misidentification).

Ocellar - ocular interspace 0.2 to 0.5 times interocellar space; posterior ocellus to occipital carina a little greater to nearly twice longer than first flagellar segment and a little narrower to distinctly wider than diameter of a posterior ocellus; maximum length of temple much shorter than greatest transverse diameter of compound eye, subequal to much longer than first flagellar segment; posterior sulci of stemmaticum deep, tending to join middorsal sulcus behind the posterior ocelli; lateral sulcus of stemmaticum generally absent; occipital carina usually squared or dipped centrally on vertex. Gena from less than 0.4 to about 0.6 times width of mandible base; postgena distinctly longer than genal inflection, latter 0.4 to 0.7 times width of mandible base. Sculpture of epistoma not markedly different from that of facial orbits; last two segments of maxillary palpus about equal in length. First flagellar segment 3.5 to over 4.0 times longer than its maximum width. Range: 40 to 49 segments.

Mesonotum with fine punctures; body frequently yellow patterned, especially with "vittate" mesonotum; pleurosternal angle of epicnemium very strongly obtuse; mesopleural punctures sparse, interspaces not strongly microsculptured.

Wings with submedian cell somewhat evenly trichose, nervellus of hind wing distinctly reclivous above; substigmal speculum not extending beneath prestigma; radius somewhat thickened towards base, wide angled with top edge of wing. Forewing length: 8—11 mm.

Hind femur rather thick, trochantellus short, tibial spinules moderate; mid tibial spurs strongly unequal.

Propodeum varying from near lack of carinae to a condition where only those anterior to the posterior transverse carinae are reduced. Carina lateralis generally in evidence.

Petiolar membrane just behind line of petiolar spiracles; gaster sometimes darkened at apex.

Variation. — The only really significant variation lies in the extent of the yellow markings, which may be very profuse or quite absent. Gauld (1978) states that no transverse carinae occur on the propodeum, but these are frequently present — with a maximum development as indicated in the figure (fig. 5).

Remarks. — Morley (1915) used the name *parvulus* Kr. for non-yellow marked examples of *minutus*. Townes et al. (1965) synonymises these two species, presumably as a result of the

discovery that authors had followed Morley; Perkins had examined the Kriechbaumer type and found his *parvulus* to be quite different from that of the Morley interpretation (MS). See also remarks under *parvulus* Kr. in the present work.

There should be no difficulty in recognising the present species from the key.

Biology. — A parasite of Geometrid moths, the adults of which fly during the winter month (*Erannis* species). The parasite is on the wings during May and June. It is attracted to light, and is quite frequently collected during the daylight hours. The chief habitat seems to be deciduous (and particularly Oak dominated) woodland, but includes suburban gardens.

Material examined. — 10 ♀, Wytham, Berks, 28.v.—9.vi.1967, 68, M.V. trap (M. C. Birch); 1 ♀, Low Moss Plantation, Glasgow, 1.vi.1966; 1 ♀, Cadder Wilderness, Glasgow, 23.v.1966; 2 ♂, Wytham, Berks, M.V. trap, 28.5.1968; 1 ♂, Pinner, Middlesex, 13.vi.1975, at light; 1 ♂, Low Moss Plantation, Glasgow, 19.v.1966 (all coll. J. P. Brock, unless otherwise stated); 1 ♂, Minstead, New Forest, 22.v.1976, M.V. trap (L. W. Siggs) (BMNH); 1 ♂, 1 ♀, Byfleet, SR, 26—29.v.1949 & 9—11.v.1947 (R. B. Benson) (BMNH); 2 ♂, 1 ♀, Bricket Wood, HT, 31.v.—5.vi.1951 (R. B. Benson) (BMNH); 1 ♂, Minstead, New Forest, M.V. trap, 22.v.1966 (L. W. Siggs) (BMNH); 2 ♂, Whetstone, HT, 12.v.1961 (MV) & 30.v.1959 (P. H. Ward) (BMNH); 1 ♂, Blean Wood, Kent, 20.v.1973 (BMNH); 1 ♂, Abbot's Wood, Sussex, 29.5.1932 (H. Donisthorpe) (BMNH); 1 ♀, Claygate, Surrey, 4.vi.1952 (D. M. S. Perkins) (BMNH). Reared material: "*H. progemmaria*, New Forest", 19.vi.1916 (Lyle) (BMNH); "*H. aurantiaria*, about 7.v.1902" (Morley coll.) (BMNH). At the time of writing, I have a few live cocoons of a small *Ophion* which can only be this species, from *Erannis defoliaria* (Clerck). These were from host larvae on Oak, May 1979, Copse Wood, Ruislip, nr. London.

Ophion ventricosus Gravenhorst
(fig. 6a)

Ophion ventricosus Gravenhorst, 1829: 702. Morley, 1915. Gauld, 1978.
Ophion impressus Thunberg, 1822: 262 (pre-occ). Perkins, 19-- (MS). Gauld, 1973, 1976. Oosterbroek, 1978.

Ocellar-ocular interspace 0.6 to 1.0 times interocellar space; posterior ocellus to occipital carina 1.5 to 2.0 times maximum width of first flagellar segment and up to nearly 2.0 times diameter of a posterior ocellus; maximum length of temple up to a little less than greatest transverse diameter of eye, distinctly longer than first segment of flagellum. Stemmaticum with deep posterior sulcus, no lateral sulcus. Middorsal sulcus deep. Occipital carina rounded, squared or dipped on vertex. Gena 0.4 to 0.6 times width of mandible base; postgena 1.3 to 3.0 times length of genal inflection, latter 0.3 to about 0.6 times width of mandible base. Epistomal punctures sparser than those of facial orbits. Last two segments of maxillary palpus unequal in length. Dorsal edge of mandible basally wider than a tooth. First flagellar segment from 2.5 to around 3.6 times longer than maximum width. Flagellum with 48 to about 55 segments (mean of 53).

Mesonotum with large deep puncturation, deep reddish rather than usual testaceus colour; pleurosternal angle of epicnemium very obtuse and weakly defined. Mesopleural punctures large and deep. Scutellum sometimes with lateral carinae defined. Thoracic pattern fig. 6a.

Submedian cell of forewing with evenly distributed trichiae; nervellus slightly reclivous above; substigmal speculum not extending beneath prestigma; radius slightly thickened towards base. Wings somewhat orange-tinted. Forewing length: 8—14mm.

Hind femur rather stout, tibial spinules moderate, hind trochantellus short; mid tibial spurs distinctly unequal.

Propodeum with most of the carinae generally in evidence, including carina lateralis. The costulae are discrete from the usual transcarina in this region. The propodeum is usually marked with black.

Abdomen generally darkened towards apex; membrane of petiolar segment well behind line of spiracles.

Variation. — There is no really significant variation in this species, other than that involving the greater or lesser extent of the black markings of the head, thorax, propodeum, abdomen and legs.

Remarks. — This species is unlikely to be mistaken for any other European member of the genus.

Biology. — W. Watson has reared this species of *Ophion* through the Geometrid *Apocheima pilosaria* (D. & S.). Habitats of captured adults seem usually to be deciduous woodland. It is a widely distributed species, of rather sporadic

occurrence. Records extend to Loch Lomond-side in southern Scotland, but *Ophion ventricosus* appears to be absent from many localities which contain large populations of the above host.

Material examined. — 1 ♂, Garth, Loch Lomond, Scotland, 21.vi.1964, M.V. trap (K. Stewart) (BK); 2 ♂, 3 ♀, Bricket Wood, Herts., 27.vi.1948, 20.v.1947, 23.v.1939, 4.vi.1951 (R. B. Benson) (BMNH); 1 ♂, New Forest, 8.v.1960 (J. F. & R. A. Perkins) (BMNH); 1 ♂, Rammamere Heath, BX, 31.vi.1950 (R. B. Benson) (BMNH); 1 ♂, Woodwalton Fen, Hunts., 12—14.v.1958 (R. B. Benson) (BMNH); 1 ♂, Wenlock Edge, Shropshire, 24.vi.1958 (J. F. Perkins) (BMNH); 1 ♂, Leamington Spa, WW., 10.viii.1954 (M. Bibikoff) (BMNH); 1 ♂, Oxshot, Surrey, 24.v.1936 (J. F. Perkins) (BMNH); 1 ♂, Byfleet, Surrey, 9-11.v.1947 (R. B. Benson) (BMNH); ex. *Apocheima pilosaria* (D. & S.): 1 ♀, 2 ♂, host coll. v/vi.1975, adult emerged vi.1976 (W. A. Watson) (Shaw coll.); further British records can be found in Morley (1915).

Ophion scutellaris Thomson
(figs. 7—9)

Ophion scutellaris Thomson, 1888: 1192 (lectotype, Lund). Perkins, 19-- (MS). Gauld, 1973, 1976, 1978. Oosterbroek, 1978.
Ophion longicornis Brauns, 1889. Schmiedeknecht, 1908. Morley, 1915.
Ophion stigmaticus Morley, 1915.

Ocellar-ocular interspace from less than 0.2 (females) to about 0.65 (males) times interocellar space; posterior ocellus to occipital carina 1.0 to 1.6 times width of first flagellar segment and 0.5 to around 1.0 times diameter of a posterior ocellus. Maximum temple length much shorter than greatest transverse diameter of eye and 0.7 to 1.0 times length of first flagellar segment. Sulci of stemmaticum complete, lateral sulcus often deeper than middorsal sulcus. Mandibular flange subglabrous, gape not acute, internal angles sharp. Surface of mandible noticeably deplanate. Occipital carina generally rounded or squared, not angled centrally. Gena around 0.4 (female) to nearly 0.8 (male) times width of mandible base; postgena 0.6 to 1.8 times genal inflection, latter generally around 0.7 times width of mandible base. Eyes convergent in frontal view; facioclypeal area subquadrate to transverse; epistoma tending to be more sparsely punctured than orbits; last two

segments of maxillary palpus unequal. Antennae unusually elongate; first flagellar segment 3.6 to over 4.0 times longer than broad. 62 to 72 flagellar segments.

Thorax with fine puncturation, weak microsculpture; mesonotum often with darkened areas; pleurosternal angle of epicnemium sharp, rectilinear to obtuse, not aligned with sternal angles. Scutellum often with strong lateral carinae.

Submedian cell of forewing somewhat evenly trichose (variable); nervellus not reclivous above; substigmal speculum not clearly produced beneath prestigma; radius sinuate towards base. Forewing length: 14—18 mm.

Hind coxa and femur elongate, former small in relation to lateral area of propodeum. Trochantellus short. Tibial spinules only rudimentary. Mid tibial spurs of only slightly unequal length (1 : 0.8 or more).

Propodeum with carina lateralis, lacking complete area superomedia and dentiparae (and sometimes the carina lateralis). Keel between latter and spiracle often absent.

Petiolar membrane far behind line of spiracles.

Variation. — The keel joining the lateral carina to the propodeal spiracle was found to be present in roughly thirty percent of specimens and its absence cannot therefore be used as a diagnostic feature of the species as indicated by Gauld (1978). The other characters given by that author are more reliable and are those brought forward by Perkins, in his manuscript key to *Ophion* (but see *obscuratus* flagellar variation!).

Remarks. — Perkins found that specimens placed under the name *scutellaris* Ths. in the Morley collection were in fact referable to *pteridis* Kr. He also recorded that Morley had used the name *longicornis* Brauns for the present species. This synonymy was later checked and published by Gauld (1973, 1976). Perkins also indicated that Morley's own *O. stigmaticus* was a form of *scutellaris* Ths. (see Gauld 1973, 1976).

There should be no difficulty in identifying this species, as it is on the wing well before any other with which it might be confused. Early specimens of *obscuratus* may however be taken along with it; these will generally be recognised by their yellow markings or by the shorter flagellum of the latter species. Two of the paratype specimens of *stigmaticus* that were redetermined by Gauld (loc. cit.) as *scutellaris* are in fact refer-

able to *obscuratus*. A further two paratypes from the Morley *stigmaticus* material, stated by Gauld to be *luteus* (sensu Perkins — Gauld) are males of *parvulus* and *obscuratus* respectively.

Biology. — Hosts are overwintering Noctuid larvae which reach near-maturity in spring. Normally, they appear to feed on grasses or other low plants of open ground (meadows, commons, heaths, and woodland clearings). The parasite is often seen flying in sunshine in such habitats, and is probably common in most suitable localities throughout Britain.

Material examined. — 3 ♀, 8.v.1965, 15.iv.1964, 10.iv.1963, Minstead, New Forest, M.V. trap (L. W. Siggs) (BMNH); 3 ♂, 3 ♀, same data as above (13.iv.1974—iv.1975) (BK); 2 ♀, Freshfield, Lancs., 9.iv.1964 (C. O'Toole) (BK); 3 ♀, Wytham Wood, Berks., M.V. trap (M. C. Birch) (BK); 3 ♀, Wytham, Berks., M.V. trap, v.1967/68 (BK); 1 ♀, Milngavie, Glasgow, 11.v.1966 (common in this locality) (BK); no data (? Lancs.) (C. O'Toole) (BK); several males observed at Shabbington Wood/Waterperry Wood, near Oxford, 1968/69 (BK); 2 ♂, 2 ♀, Minstead, New Forest, M.V. trap, 2.iii.—27.iv.1966 (L. W. Siggs) (BMNH); 1 ♂, Oxenbourne Down, Hants., 1.iv.1973, M.V. trap (G. Else) (BMNH); 1 ♀, Dartford Heath, Kent, 1—7.iv.1958 (R. L. E. Ford) (BMNH); 1 ♂, 1 ♀, Glen Brittle, Skye, W. Ross, 20—21.iv.1962 (L. Horacsek) (BMNH); 2 ♂, Arkley, HT., 9.iv.1953 (T. G. Howarth) (BMNH); 1 ♀, Kent's Oak, Romsey, Hants., 6.iv.1969, at light (C. R. Vardy) (BMNH); 1 ♂, Wimbledon Common, Surrey, iv.1958 (J. A. & D. J. Clark) (BMNH); reared through "*T. fimbria*" and "*N. xanthographa*", 1909, 1910 (Lyle) (BMNH); also Hayling Island, SH., ex *Aporophyla nigra* (Sperring) (BMNH).

Ophion luteus (Linnaeus)
(figs. 11—16, 41a, graphs 1, 1a, 5)

Ichneumon luteus Linnaeus, 1758 (holotype male, London; Linn. coll.). Morley, 1915. Perkins, 19-- (MS). Gauld, 1973, 1976, 1978. Oosterbroek, 1978.
Ophion distans Thomson, 1888. Morley, 1915.
Ophion ?slaviceki Kriechbaumer, 1892: 233 (lectotype male, Munich). Perkins, 19-- (MS). Gauld, 1976, 1978.
Ophion calcaratus Morley, 1915.

Ocellar-ocular interspace usually in range 0.2—0.6 times interocellar space (sometimes much shorter); posterior ocellus to occipital carina 1.3 to 2.0 times maximum width of first flagellar segment and from 0.6 to over 1.0 times diameter of posterior ocellus; temple with maximum length distinctly shorter than greatest transverse diameter of eye, usually 1.0 to 1.3 times length of first flagellar segment; sulci of stemmaticum more or less complete, sometimes with a stemmatico-ocular line to eye; occipital carina usually rounded or squared, but sometimes weakly angled centrally. Gena around 0.4 to as much as 0.9 times width of mandible base; postgena 1.0 to 1.8 times length of genal inflection, latter 0.7 to 0.8 times width of mandible base. Eyes weakly divergent in frontal view; facioclypeal area moderately to strongly transverse; mandible elongate, usually with acute gape, weak to absent internal angles to the teeth, the flange with distinct medial punctures. Punctures of epistoma similar to or of *sparser* distribution, than those of orbits; last two segments of maxillary palpus unequal in length. First segment of flagellum usually around 4.0 times longer than broad (may be much shorter, or even more elongate than this); usual range of flagellar segments, 52—59 (mean 54 in male, 56 in female): see also remarks below.

Thorax with shallow puncturation and weak microsculpture; mesonotum sometimes with weak yellow "vittae"; pleurosternal angle of epicnemium usually obtuse, not aligned to sternal angles. Lower sector of pleural epicnemium up to about 0.5 times upper sector. Scutellum rarely with trace of carinae.

Submedian cell of forewing sparsely trichose above, but sometimes evenly trichose. Substigmal speculum more or less extending beneath prestigma; stigma not yellow apically; radius sinuate towards base. Forewing length: 10—18 mm.

Hind femur moderately elongate, trochantellus as long or longer than minimum width. Hind tibia with strong spinules. Mid tibial spurs moderately to very strongly unequal in length.

Carina lateralis absent to weaker than dorsal propodeal carinae. Superomedia and dentipara incomplete.

Membrane of petiolar segment near line of spiracles.

Variation. — An exceedingly variable species, especially in head characters. There is wide overlap with the *longigena* subgroup in more buccate headed individuals, but these can be distinguished on characters given in the key. Gen-

erally speaking, *luteus* is characterised by the form of the mandible, lack of scutellar carinae, elongate hind trochantellus and non-angulate vertex. Since all of these characters are subject to variation and exception, any doubtful specimens should be compared point by point with the description. Confusion with *obscuratus* is possible, since some forms of *luteus* may be yellow marked (and *obscuratus* not). Overlap with related species is however, not too frequent and the key has been constructed to deal with most variants which will be encountered. Specimens with unusually small ocellar-ocular interspace may be confused with *parvulus*, but these can be eliminated on the form of the hind trochantellus.

Sexual dimorphism is quite marked in this species, the greater extremes of variation in most characters being attained most frequently by males.

Remarks. — Thomson separated his *O. distans* on the basis of characters which are certainly unreliable and which occur in any combination within contiguous populations of *luteus*. The subsequent history of *distans* is as follows:

(1) Perkins found that the Linnaean type of *luteus* was in fact of the *distans* form; since he regarded this as a good species, Perkins used the first available name, *slaviceki* Kr. for *luteus* auctt. nec L. and placed *distans* as a synonym of *luteus* L. (unpubl. MS).

(2) Gauld (1973, 1976, 1978) published the Perkins findings, at the same time re-examining the types. Unfortunately, he did not look fully into the question of infraspecific variation in these insects. As a result, the name *slaviceki* Kr. has gained currency for the *O. luteus* of authors.

(3) Following analysis of characters used to separate *luteus* and "*distans*", together with study of material named by Perkins in the British Museum collections, I came to the conclusion that *luteus* and *slaviceki* were simply variants of a single species.

(4) I have seen the type of *slaviceki* Kr., but am not satisfied that the specimen so designated agrees with the description given by Kriechbaumer (1892). It is a typical specimen of *luteus*, lacking the unusual features of *slaviceki* as given by the describer (loc. cit.).

(5) Oosterbroek (1978) places *slaviceki* Kr. sensu Gauld as a synonym of *luteus* L. He is in agreement with the present author concerning the unreliability of characters used to split *luteus*.

Gauld (1976) discusses the synonymy of *O. calcaratus* Morley with *slaviceki* Kr. — Gauld.

The identity of the true *slaviceki* remains an open question, unless it can be shown that the lectotype was the specimen from which Kriechbaumer drew his original description.

Specimens of *luteus* sensu Perkins in the National collection are smaller on average and have fewer flagellar segments than normal *luteus* specimens. For the most part, they also have earlier dates of capture than the latter. From a regression curve of wing length on flagellar segment number (graph 5 and 1a), these individuals
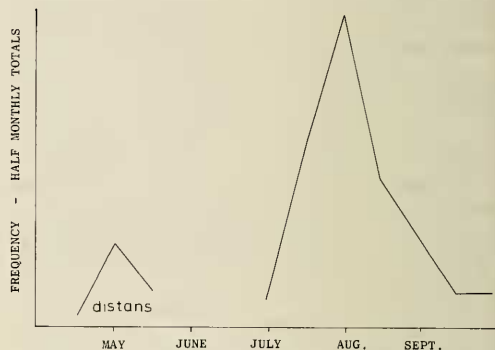
Graph 1. Temporal frequency distribution for *Ophion luteus* (L.).
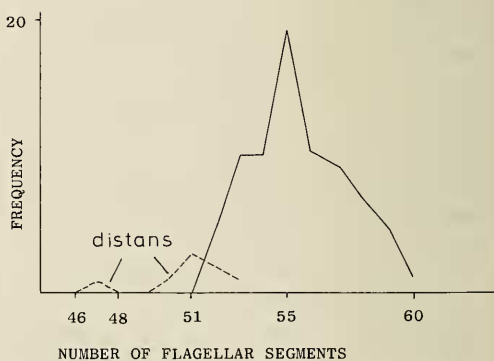
Graph 1a. Flagellar segments frequency distribution for *Ophion luteus* (L.).

would seem to be a simple downwards extrapolation of the usual *luteus* (sensu lato) trend — very possibly representing an occasional, seasonal, host-correlated dimorphism in the species — as observed for the related *obscuratus*.

The only *luteus* sensu stricto material named

by Gauld that I have seen, were the two already referred to under *scutellaris:* these were misdeterminations of two other species.

Biology. — Apart from the rearing of some *luteus* sensu Perkins-Gauld through the duneland Noctuid *Ochropleura* (*Agrotis* sens. auctt.) *praecox* (L.), I have been unable to trace any authentic rearing of this species. This is remarkable, since *luteus* is the commonest species of the genus, and is found in almost any kind of habitat. Circumstantial evidence would seem to suggest that the host is some Noctuid larva of such frequent occurrence that it is seldom reared by Lepidopterists! From the *distans* rearings, this could well be an overwintering larva — but the temporal frequency distribution of adult *luteus* is very similar to that of *pteridis* (which attacks hosts which overwinter as pupae, not larvae).

Material examined. — 36 ♂, 55 ♀, Minstead, New Forest, M.V. trap, vii/viii/ix.1963—75 (L. W. Siggs) (BMNH/BK); 5 ♀, Whetstone, 23.viii—5.x.1959 (P. H. Ward) (BMNH); 1 ♀, Sudbury, 4.ix.1925 (P. Harwood) (BMNH); 1 ♀, Romsey, Kent, 17—21.ix.1963 (C. R. Vardy) (BMNH); 1 ♀, Beckenham, Kent, 14.viii.1963 (R. I. Vane-Wright) (BMNH); 1 ♂, Whetstone, 25.vii.1959 (P. H. Ward) (BMNH); 2 ♀, Woodchester Park, Gloucs., ix.1972 (BK); 3 ♀, Solihull, Birmingham, 17—18.vii.1969 (M. R. Shaw) (BK); 8 ♂, Solihull, Birmingham, M.V. trap, 17—24.viii.1969 & 29.viii.1973 (M. R. Shaw) (BK); 1 ♂, Cornwall, 4—10.viii.1974 (J. St. E. Cardew) (BK); 2 ♂, Sanderstead, Surrey, 22.viii.1950 (R. W. Crosskey) (BMNH); 1 ♀,

British Museum, 12.ix.1925 (J. Waterston) (BMNH); 1 ♂, Hayes, Kent, 18.viii.1963 (A. Banks) (BMNH); 1 ♂, Colchester, NE., 17.viii.1952 (D. De Havilland) (BMNH); 1 ♂, Keston, WK., 11.ix.1949 (A. E. Wood) (BMNH); 1 ♀, Kent's Oak, Romsey, Hants., at light, 7.x.1972 (C. R. Vardy) (BMNH); 1 ♀, Beckenham, Kent, 30.viii.1966 (R. I. Vane-Wright); 1 ♀, Tooting Common, Surrey, at light, 10.ix.1924 (O. G. Heath) (BMNH); 1 ♀, Botley Wood, Hants., 9.x.1974 (G. R. Else) (BMNH); 1 ♀, nr. Stroud, Glos., 23.ix.1960 (A. C. Pont) (BMNH); 1 ♀, Arkley, Hants., M.V. trap, 22.viii.1954 (Sir L. Wakely) (BMNH); 1 ♀, Digby, Lincs., 20.ix.1958, at light, 20.ix.1958 (C. R. Vardy) (BMNH); 1 ♀, Juniper Hall, Boxhill, Surrey, 18.ix.1963 (R. G. Adams) (BMNH); 1 ♀, Parlock, 16.viii.1956 (D. M. S. Perkins).

Material of *luteus-distans* in coll. BMNH: 2 ♂, Elveden, Suffolk, 2.vi.1911 (Nurse); 1 ♂, Milton, Cambs., 28.v.1924 (Benson); 1 ♂, Gairloch, Scotland, 9.vi.1958 (Benson); 2 ♂, 1 ♀, Monk's Soham, 31.v.1909, reared (? host) (Morley); 1 ♂, 12.viii.1906, no other data (Morley); 1 ♀, no data (Stephens coll.); 1 ♀, "Clutten" (Harwood); 4 ♂, 1 ♀, Hunstanton, 27.v.1918, ? 3.v.1918, 25.v.1918 (Lyle).

Ophion obscuratus Fabricius
(figs. 6b, 17b, 19—22, graphs 3, 4a—b)

Ophion obscuratus Fabricius, 1798: 237 (lectotype male, Copenhagen). Perkins, 19-- (MS). Gauld, 1973, 1976, 1978. Oosterbroek, 1978.
Ophion obscurus Fabricius, 1804. Schmiedeknecht, 1908. Morley, 1915.
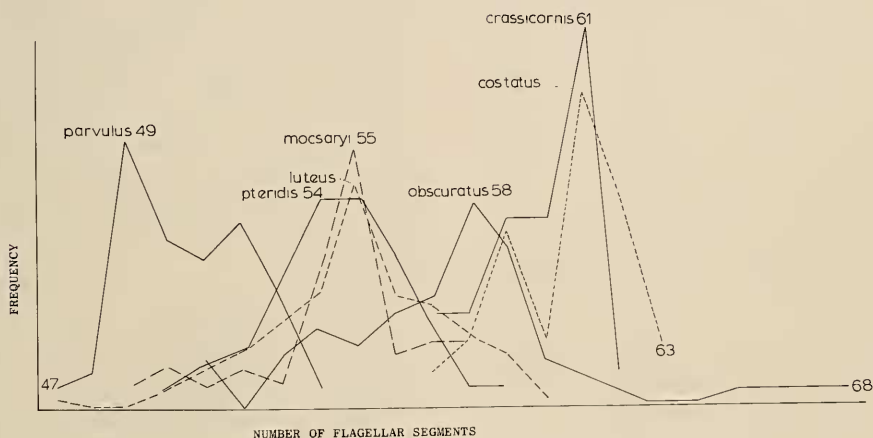
Graph 2. Flagellar segments frequency distribution for seven critical *Ophion* species (relative frequency values).

Ocellar-ocular interspace less than 0.2 to (sometimes) 0.6 times interocellar space; posterior ocellus to occipital carina 1.0 to 1.7 times maximum width of flagellum 1, 0.5 to 0.7 times diameter of posterior ocellus. Temple with maximum length always distinctly shorter than greatest transverse diameter of eye, subequal to length of first segment of flagellum; stemmaticum with complete sulci, lateral sulcus often weak or erased. Stemmatico-ocular line sometimes present. Occipital carina weakly to sharply angled centrally. Gena 0.3 to rather more than 0.4 times width of mandible base; postgena less than, or equal to length of genal inflection, latter 0.7 to 1.0 times width of mandible base. Mandible with rectangular to obtuse gape, sharp internal angles to the teeth, flange generally with distinct punctures medially. Epistomal punctures similar to, or closer together than on orbits. Last two segments of maxillary palpus unequal in length. Dorsal edge of mandible as wide as a tooth. First flagellar segment approximately 3.0 to a little over 4.0 times longer than broad. Usual range of 54—62 flagellar segments (mean of about 58). See remarks on variation below.

Mesonotum not strongly punctate, often vittate. Yellow markings often spreading to pleuron, propodeum, abdomen. Pleurosternal angle of epicnemium often obtuse, rarely acute, usually somewhat rounded. Not aligned with sternal angles. Mesopleural punctures moderately close, with distinctly microsculptured background. Scutellum without distinct lateral carinae.

Forewing with evenly distributed trichiae on submedian cell; substigmal speculum more or less extending beneath prestigma; stigma usually yellow at apex; radius sinuate towards base. F.wg.: 10—18 mm.

Hind femur quite slender, trochantellus around same length as its minimum width in dorsal view. Tibial spinules quite strongly developed. Mid tibial spurs moderately unequal in length, sometimes strongly so.

Propodeum sometimes with area basalis defined, rarely with trace of dentiparal carinae; superomedia incomplete, carina lateralis rather weak, usually less developed than more dorsal carinae.

Membrane of sternite of petiolar segment approximately in line with spiracles. Tergite 3 up to 3.0 times wider at apex than at base.

Variation and biology. — The unusually wide
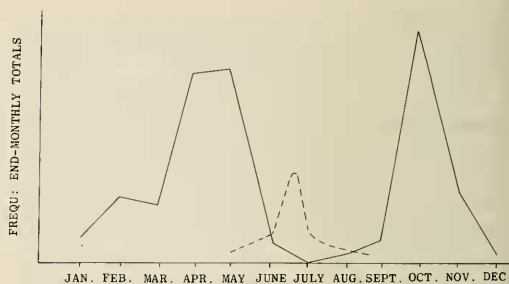
Graph 3. Temporal frequency distribution for *Ophion obscuratus* F. *O. crassicornis* sp. nov. shown for smaller sample.

spectrum of variation found with regard to structure and colour in this species points to a seasonal (and probably at least partially host-correlated) polymorphism. This is reflected for example, by the frequency distribution of flagellar segment number (graph 4a), and by the strongly trimodal frequency distribution for wing length in a large, quasi-random sample (graph 4b). The three morphs can be roughly categorised as follows:

(1) Spring form — wing length 13—15/16 mm, 54—60 flagellar segments. Ocellar-ocular interspace usually in the range: 0.2 to 0.4 × interocellar space. Distance between posterior ocellus and occipital carina much greater than width of first flagellar segment; testaceous with moderately distinct yellow markings. Hosts medium-sized Noctuidae, frequenting more open habitats and woodland clearings. Flies both in sunshine and at night, common. Feb. to June.

(2) Autumnal "giants" — wing length 15/16—18 mm, 56—68 flagellar segments; ocellar-ocular interspace usually 0.1 to 0.3 × interocellar space; posterior ocellus to occipital carina not much greater than width of flg. 1. Colour tending towards infuscate-testaceous, with very vivid yellow markings. Hosts unknown. Abundant, particularly so in gardens in both urban and suburban localities. Most usually attracted to light, rather than being captured in daylight. August to February, including the winter months.

(3) Autumnal "dwarfs" — wing length 10—13 mm, 51—58 flagellar segments; posterior ocellus to eye, 0.35—0.6 × interocellar space. Posterior ocellus to occipital carina 1.25—1.7 × width of flg. 1; colour reddish-testaceous, most often with weak, or no yellow patterning (excepting usually, the stigmal apex). Hosts small
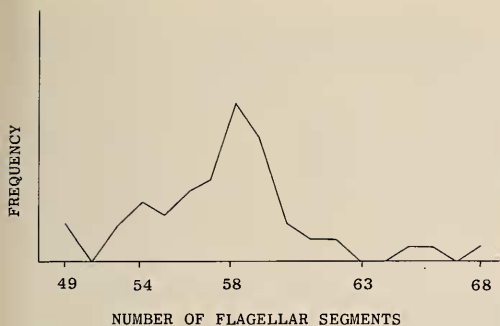
Graph 4a. Flagellar segment frequency distribution for *Ophion obscuratus* F.
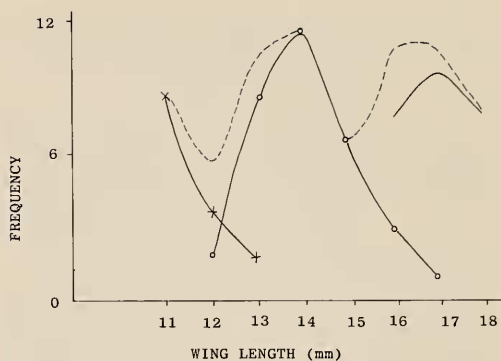

Graph 4b. Wing length frequency distribution for *Ophion obscuratus* F. (Continuous line: 3 morphs separately; broken line: combining all morphs.)

Noctuidae on heathland. Sporadic, but of widespread distribution; sometimes common. August to February.

Winter records for the "autumnal" morphs do not refer to hibernating individuals, since both sexes have been taken on the wing during December and January. A long, staggered emergence period is therefore likely for these "late" forms. From the available host data, it seems very likely that host choice is strongly correlated with structural polymorphism in this species. The stable spring population attacks its hosts early in the year, but adults do not emerge from spring cocoons until the following year. This has been shown to be the case from my own experience, independently confirmed by
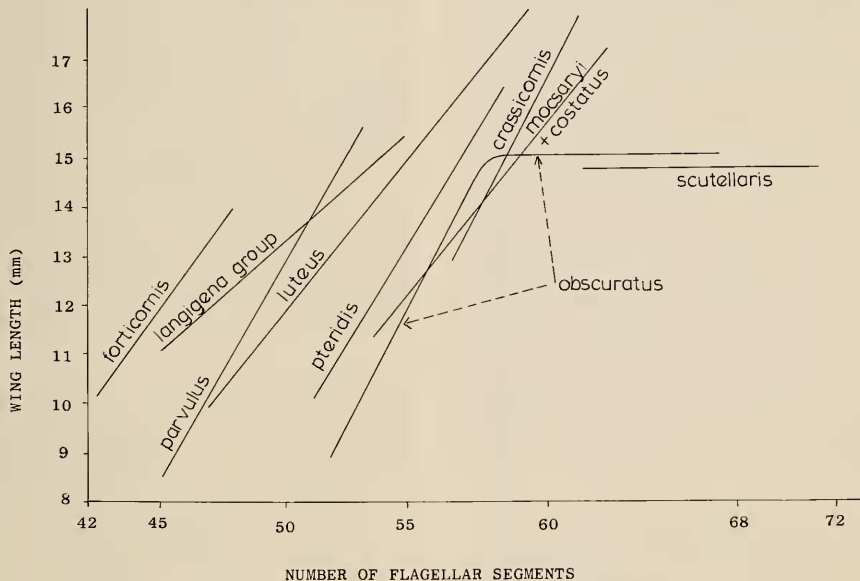
species	P levels	species	P levels
forticornis	<0.05	crassicornis	<0.01
longigena gp.	<0.001	obscuratus (a)	<0.001
parvulus	<0.001	obscuratus (b)	N.S.
luteus	<0.001	scutellaris	N.S.
pteridis	<0.001	mocsaryi/costatus	<0.001

Graph 5. Regression of flagellar segment number with wing length for the *Ophion luteus* complex.

M. R. Shaw (pers. comm.). Several facts do however, seem to support the view that biologically distinct species are probably not responsible:

(a) From a regression analysis of wing length on number of flagellar segments taken across all forms of obscuratus (graph 5), it was shown that these two characters are directly correlated (probably as a simple growth function) for small to medium-sized individuals, irrespective of other characteristics (including times of appearance). Unusually large individuals show no such relationship, flagellar segment number varying quite independently of wing length. A similar analysis was done for most other Ophion species, the results showing that the form of direct linear relationship of the two variables studied is the usual one taken by a graph of wing length plotted with flagellar segment number. This was not the case with scutellaris, however. I interpret this as follows: flagellar segment number and wing length are directly correlated with each other due to the fact that both are correlations of a simple growth function. In unusually large individuals (or in species such as scutellaris in which there is always an unusually large number of flagellar segments) there is a relaxing of the canalizing selection normally acting to hold genetic or environmentally induced variation of flagellar segment number within tolerable limits, so that such variation is allowed a certain degree of expression independently of growth function relationships. This fits very well with the widely known fact that greater variation is observed in multiple-compartmentalised structures following a serially homologous form. Smaller "autumnal giant" obscuratus forms merge with larger spring forms, in their agreement with expected regression in the two characters studied. In contrast, members of the pteridis-parvulus species pair show very widely displaced regression lines for the same variables. Thus, there is at least some indication of polymorphism rather than speciation between morphs of the present species.

(b) Since the dwarf form of obscuratus seems to be the best defined morph, some further investigation is necessary in this area. This morph also fails to produce large enough forms for any example to fit into the "grey area" of the regression analysis. Since rearing records of this morph were from Lycophotia varia, and since the form appears always to be collected in localities frequented by this moth, it seemed appropriate to test whether or not females collected

from heaths would show any preference between hosts offered in captivity. Two females of this form were taken at Chobham Common in October, 1979 and offered larvae of L. varia, M. impura (certainly one host of the spring brood of obscuratus) — together with two other "remote" Noctuids: Anarta myrtilli and Apamea sp.; a Tenthredinid larva was also offered as a "control". The result was that oviposition was attempted many times in all species of Noctuid larvae, apparently without preference. The sawfly larvae were completely ignored. This does not prove that such non-preference necessarily happens in the wild state, nor that development of parasites can take place in all attacked hosts. Of rather more significance from the point of view of interpreting variation in the parasite species, is the fact that, (a) parasite adults showed no apparent preference for larvae at different stages in their development, attempting oviposition in third to final instar hosts of several species; (b) known hosts of O. obscuratus are peculiar for the fact that they themselves possess a staggered growth period. Both small and large larvae of L. varia were found simultaneously in the autumn, while M. impura larvae representing widely different developmental stages can be found in spring. Thus, it seems highly likely that the apparently host-correlated polymorphism of the parasite is related to this characteristic of the host species. J. F. Perkins (MS) thought it possible that the dwarf form at least could be specifically distinct, while Gauld (1978) does not take this morph at all into account in his key to the British Ophion species. This form also appears to have some points in common with the O. subarcticus of Hellen, also kevoensis (see Jussila, 1976).

Material examined. — 13 ♂, 9 ♀, Minstead, New Forest, 1963—75 (L. W. Siggs) (BMNH) (BK); 7 ♂, Bingley, St. Ives — data incomplete (J. Wood) (MU); 5 ♂, Lichfield — data incomplete (Carr) (MU); 1 ♀, Formby Pt., Lancs., 16.xi.1950, ex Triphaena comes, emerged 4.iii.1951 (K. C. Greenwood) (MU); 1 ♂, Delamere, Cheshire, 19.x.1924 (H. Britten) (MU); 1 ♂, Skirwith, Cumbs., 19.ix.1926 (H. Britten) (MU); 1 ♂, Chat Moss, Lancs., 8.x.1933 (H. Britten) (MU); 1 ♂, Witherslack, 16.v.1925, no other data (MU); 1 ♂, Longdendale, Cheshire, 16.x.1932 (H. Britten) (MU); 1 ♂, Hale, Cheshire, 21.v.1922 (H. R. P. Collett) (MU); 1 ♂, 2 ♀, Staley, Cheshire, 22.x.1939 (H. Britten) (MU); 2 ♂, Wytham, Berks., M.V. trap (M. C.

Birch) (BK); 1 ♂, Rutland, 2.v.1974 (J. St. E. Cardew) (BK); 1 ♂, Waterperry Common, nr. Oxford, 9.v.1968 (BK); 1 ♂, Wytham, Berks., M.V. trap, 2.vi.1969 (BK); 1 ♀, Oxford, 22.x.1968 (R. B. Angus) (BK); 1 ♀, Oxford, 25.x.1967 (I. Lansbury) (BK); 1 ♀, Ruislip Common, nr. London, ex *Mythimna impura* larvae, vi.1975, emerged iii.1976 (BK); 7 ♂, 5 ♀, Whetstone, Herts., 27.iv.—10.v.1959, 7—12.x.59, 5.v.60 (P. H. Ward) (BMNH); 1 ♂, Esher, Surrey, x.1945 (BMNH); 1 ♂, Worcester Park, Surrey, at light, 28.ii.1960 (R. D. Eady) (BMNH); 1 ♂, 1 ♀, Beckenham, Kent, 19.x.1966 (R. I. Vane-Wright) (BMNH); 1 ♂, Sinam Common, Hants., 18.iii.1972 (coccoon), adult 19.iv.1972 (G. R. Else) (BMNH); 1 ♂, Arkley, HT., 23.iii.1954 (T. G. Howarth) (BMNH); 1 ♀, Weybridge, Surrey, v.1951 (E. Taylor) (BMNH); 1 ♀, Banstead, Surrey, at light, 27.3.1951 (S. Wakely) (BMNH); 1 ♀, Hurt Wood, Surrey, 12.v.1954 (R. B. Pike) (BMNH); 1 ♀, Catisfield, Fareham, Hants., v.1971, M.V. trap (BMNH); 1 ♀, Aviemore, Inverness-shire, 2—4.vi.1934 (R. B. & J. E. Benson); 1 ♀, Bricket Wood, Herts., 23.v.1959 (R. B. Benson) (BMNH); 1 ♂, Digby, Lincs., at light, 20.ix.1958 (C. R. Vardy) (BMNH); 1 ♀, Ivinghoe, BX., 13.v.1954 (R. B. Benson) (BMNH); 1 ♂, Earl's Court, London, 23.i.1952 (Lang) (BMNH); 1 ♀, 1 ♂, Chelsfield, 20.x.1950 (A. M. Swain) (BMNH); 1 ♂, Parks Fence, Oxford, 30.x.1926 (BMNH); 3 ♂, 9 ♀, New Forest, SH., "ex *strigula*" (L. porphyrea), 2.x.—27.xi.1909 (Lyle) (BMNH); 2 ♀, Ainsdale, Lancs., ex *Agrochola* or *Xanthia* sp., host larvae coll. 5.vi.1975, parasite larvae emerged from host prepupa, vi.1975, adults emerged 2.iv. & 6.iv.1976 (M. R. Shaw coll.); 1 ♀, Lyndhurst, New Forest, SH., ex *Noctua interjecta*, host larva 19.v.1975, parasite larva from host prepupa, c.16.vi.1975, adult emerged 11.iv.1976 (M. R. Shaw coll.); 5 specimens ex *Leucania impura*, 10—12.iv.1907, "Brit.Is." (P. Harwood) (BMNH); reared from *Amathes agathina*, Poole, Dorset, 24.iii.—5.iv.1914 (Lyle) (BMNH); from "*T. fimbria*", New Forest, Hants., 24.ii.1918, 23.ii.1911, iv.1903, 16.iii.1915 (Lyle) (BMNH); from "*N. neglecta*", 14.iv.1904 (Lyle) (BMNH); from *N. baja*, New Forest, Hants., 9.iii.1913 (Lyle) (BMNH); from *N. augur*, Shibden, Hx., 13.iv.1923 (Lyle) (BMNH). In addition, six males and two females were taken at Chobham Common in Surrey, 10—20.x.1979. Several others were ob-

served flying in sunshine at the same time; these were all "autumnal dwarfs".

Ophion forticornis Morley
(figs. 17a, 18)

Ophion forticornis Morley, 1915: 270—271 (lectotype, London). Perkins, 19-- (MS). Gauld, 1973, 1976, 1978. Oosterbroek, 1978.
Ophion? baueri Habermehl, 1930: 114.

Ocellar-ocular interspace less than 0.4 (female) to over 0.6 (male) times interocellar space; posterior ocellus to occipital carina around twice maximum width of first flagellar segment, 0.8 times to about equal to diameter of posterior ocellus; temple distinctly shorter than greatest transverse diameter of eye and subequal to length of first flagellar segment; stemmaticum with mid-dorsal sulcus stronger than lateral sulcus; stemmatico-ocular line indistinct. Occipital carina sharply angled centrally. Gena from 0.35 (female) to nearly 0.8 (male) times width of mandible base; postgena a little less to a little greater than length of genal inflection. Latter over two thirds width of mandible base. Facioclypeal area more or less transverse; mandible as *obscuratus*; epistomal sculpture also as *obscuratus*; last two segments of maxillary palpus unequal; first flagellar segment 4.0—4.5 times longer than broad, 43 to 49 flagellar segments (small sample). Antenna appearing rather short and stout, with subquadrate central segments.

Mesonotum weakly to moderately strongly punctate; colour similar to *obscuratus*, but no non-yellow marked specimens seen. Pleurosternal angle of epicnemium subrectangular, more nearly aligned to sternal angles than in *obscuratus*. Mesopleural punctures about as far apart as their diameter. Scutellum not carinate.

Wing characters as *obscuratus*, including yellow stigmal apex. Forewing length: 10—14 mm.

Hind femur moderately slender, trochantellus about as long as wide, tibial spinules weak. Mid tibial spurs moderately to only slightly unequal in length.

Propodeum with dorsal carinae more strongly raised than normal, dentiparal and superomedial carinae tending to be more nearly complete than in *obscuratus*.

Membrane of first sternite near line of spiracles. Third abdominal tergite not more than twice as broad at apex than at base, in lateral view — abdomen thus appearing more slender than in *obscuratus* (more so in Dutch than in British material however).

Variation. — With the exception of the number of flagellar segments, the characters given by Gauld (1973, 1978), after Perkins (MS), lie within the range of variation found in *O. obscuratus*. In fact, the shape of the flagellar segments and mesonotal puncturation are unstable characters in both species. There is also overlap in the development of the propodeal carinae; the latter character was indicated by Oosterbroek (1978) as an additional feature of *forticornis*. I have also discovered overlap of this kind with regard to the additional characters which I have used to attempt clear distinction between *obscuratus* and the present species.

Remarks. — Oosterbroek (1978) is probably correct in placing *baueri* Habermehl as a synonym of *forticornis* Morley, although neither he nor I has been able to locate the type of *baueri*.

The arguments for and against retention of *forticornis* as a distinct species are as follows:

(1) Overlapping character states appear not to occur together (in combination) in individual variants of either *obscuratus* or *forticornis*.

(2) The *range* of variation (with particular reference to the number of flagellar segments) in a combined *obscuratus* — *forticornis* would be very significantly greater than one would expect within a single *Ophion* species, from study of variational range in other species of the genus. *Against*:

(3) There is no absolute structural gap between *obscuratus* and *forticornis*, other than that exhibited by the number of segments in the flagellum. This latter feature could be due to small sample of *forticornis* available.

(4) *O. forticornis* could conceivably be a duneland ecotype of *obscuratus*. In support of this would be the somewhat parallel variants of *crassicornis* and *luteus* which I have seen from similar localities; on the other hand, typical *obscuratus* forms can also be taken amongst sand dunes.

Biology. — I believe there is a specimen in the Hope Department of Entomology, Oxford, reared through *Ochropleura* (*Agrotis* auctt.) *praecox* (L.). The species flies in early summer, frequenting sand dunes (also the habitat of the host record species cited above). Rare.

Material examined. — Morley's original material came from Felixstowe, Suffolk, on sand dunes. — Holotype ♀, 6.v.1897, paratype ♀, 7.v.1900 (BMNH); I have seen one other British specimen, in the Hope Department Collec-

tions (*Dale*), reared from "*Agrotis praecox*" (see above).

The following material from Holland was sent by P. Oosterbroek, whom I contacted at the helpful suggestion of I. D. Gauld: 1 ♀, Venlo, 1877 (Oudemans coll.); 1 ♂, Venlo (Oudemans); 1 ♂, Putten, 14.v.1913; 1 ♂, Hilversum, 11.v.1893 (Oudemans); 1 ♀, Assel, 5.6.1970 (J. B. Wolschrijn).

Ophion crassicornis spec. nov.
(figs. 23, 24, graph 3)
Ophion "*species W*"; Perkins (MS).
Ophion "*species X*"; Gauld, 1978 (in part).

Ocellar-ocular interspace 0.2 to 0.5 times interocellar space; posterior ocellus to occipital carina 1.0 to 1.4 times maximum width of first flagellar segment, 0.65 to 0.8 times diameter of posterior ocellus. Maximum length of temple distinctly shorter than greatest transverse diameter of eye, usually noticeably longer than first segment of flagellum; stemmaticum with usual sulci, lateral sulcus tending to be weaker than middorsal sulcus. Stemmatico-ocular line sometimes present, may be represented by zone of rough sculpture. Occipital carina usually sharply angled centrally. Gena 0.3 to 0.4 times width of mandible base; postgena 0.65 to 1.3 times length of genal inflection, latter 0.6 to 1.0 times width of mandible base. Eyes somewhat convergent towards mouth in frontal view; facioclypeal area subquadrate; mandible with rectangular to obtuse gape, sharp internal angles to teeth, flange generally with distinct medial puncturation. Epistoma and orbits both closely punctate; last two segments of maxillary palpus unequal. First flagellar segment from less than 3.0 × longer than broad, to nearly 4.0 times (usually nearer lower end of ratio) usual range of 59 to 62 flagellar segments (mean around 60): exceptionally with as few as 57.

Mesonotum with fine puncturation; colour tending towards darker testaceous, without yellow markings. Pleurosternal angle of epicnemium generally sharply acute angled, produced backwards to nearly lie in line with sternal angles. Mesopleura closely punctured with distinct microsculpture between them. Scutellum usually carinate.

Forewing evenly trichose over submedian cell; substigmal speculum not clearly extending beneath prestigma. Forewing 12—18 mm.

Hind femur relatively stout to moderately

slender, the trochantellus much shorter than, to about equal in length to its minimum width in dorsal view; tibial spinules weaker than in *luteus*; mid tibial spurs moderately unequal in length.

Propodeum lacking area basalis, but often with closed area superomedia and dentiparal carinae indicated; carina lateralis usually weak.

Membrane subopposite spiracles of petiole. Abdomen often darkened ventrally.

Variation. — I have examined some unusual specimens of this species from northern localities. These differ from typical *crassicornis* as follows: temple shorter on average, first flagellar segment rather more elongate, nervellus broken at or below centre (tending to be broken at or *above* centre in typical specimens); noticeably smaller.

Although I have little doubt that these represent a form of *crassicornis*, I exclude them from designation as paratype material. It is possible (though uncertain as yet) that these specimens typify a form found in more open habitats, such as sand dunes or moorland. Again, they may simply represent a trend in northern populations generally.

Remarks. — This species was discovered by Perkins, who also suggested the name proposed for it. In his manuscript, Perkins placed *crassicornis* close to *longigena*. It is the same as "sp. X" of Gauld (1978) and "sp. W." of Perkins (MS). Gauld (loc. cit.) follows Perkins in placing the present species near *longigena*, but segregates within the *luteus-longigena* section will not separate satisfactorily on the characters given in Gauld's key. In particular, the trichiation of the submedian cell (as used by Perkins and Gauld) is unstable (cf. *luteus*) and the hind trochantellus of *crassicornis* is unusually variable (sometimes agreeing with *luteus*, alternately with *longigena*, following Gauld's diagnosis).

While admitting that certain similarities do exist between the present species and members of the *longigena* group, I find that there is more agreement with *obscuratus*: some non-yellow marked forms of the latter species require careful study if confusion with *crassicornis* is to be avoided. This however applies mainly to the dwarfed autumnal morph of *obscuratus*, which can generally be separated by the smaller number of flagellar segments.

Biology. — I have seen one specimen reputedly reared through the Noctuid *Aporophyla*

nigra (Haw.). The normal flight period of the parasite seems rather later than would be expected if this was the usual host. *Ophion crassicornis* seems to be increasing in numbers at about the same time as the mid-summer decline in *obscuratus* (see graph 3).

Gauld (1978) found his "species X" to be a common one, while my own experience suggests that *crassicornis* is of rather sporadic occurrence. Most probably, Gauld's view was at least partly based on the large number of specimens placed under the Perkins manuscript name in the national collection. A closer examination of these during 1979 has shown that four different species have been confused under that title. These included the "true" *crassicornis*, the "unknown" males of *brevicornis* Morl., and a Scandinavian species related to the latter. Although it now seems that *Ophion crassicornis* is rather a rare species, the existing records do suggest quite a wide distribution. Gauld also sent a specimen of "sp. X" to J. Aubert, who intended describing and naming the species on the basis of this and one other specimen. Through the very helpful cooperation of these workers, I was allowed to examine these insects, with a view to including them as paratypes of *crassicornis*. Both however, were examples of *Ophion brevicornis* Morley, thus apparently confirming the aggregate nature of Gauld's "sp. X".

Material examined. — Holotype ♂, Badbury Rings, Dorset, 4—6.vii.1955 (I. H. H. Yarrow) (BMNH); Paratypes. Minstead/Linford, New Forest, Hants., M.V. trap, 2.vi.1975, 30.vi.75, 19—25.vi.75, 6.vii.75, 7—13.viii.75 (L. W. Siggs) (BK); 6 ♂, 5 ♀, Minstead, New Forest, M.V. trap, 6.vi.1963, 3.vi.1965, 6.vi.1964, 31.v. & 5.vi.1963, 3.vi.1964, 7.vi.1964, 3.v.1964, 13.vi.1965, 17.vi.1963, 14.vii.1963 (L. W. Siggs) (BMNH); 2 ♂, Gritnam, New Forest, Hants., M.V. trap, 4.vi.1976, 28.v.1976 (BK, private coll.); reared: Hayling Island, SH., 13.vi.1961, ex *Aporophyla nigra* (A. H. Sperring) (BMNH).

Not paratypes: 1 ♂, Sicily, Segesta, 17.iv.1965, 450 m (K. M. Guichard) (BMNH); 5 ♂, 3 ♀, Spain, iv.1973, M.V. trap (J. St. E. Cardew) (BK); 1 ♂, Bolton Perry (VC64), 23.v.1943 (W. G. Blamely) (MU); 1 ♂, Stanton Sand Pits (VC61), 14.vi.1943 (W. D. Hincks) (MU); 1 ♂, Leeds Lime Hills (VC64), 28.v.1944 (J. Wood) (MU); 1 ♂, Keighley Dist. (VC63), 5.vi.1943 (J. Wood) (MU); 1 ♂, Branley Moor, Cheshire, 13.vi.1926 (A. K. Lawson) (MU).

Ophion longigena Thomson
(figs. 25—27)

Ophion longigena Thomson, 1888: 92 (lectotype, Lund). Morley, 1915. Gauld, 1978. Oosterbroek, 1978.

Ophion costatus Ratzeburg; Brauns, 1889 (? misidentification). Perkins, 19-- (MS) (in part). Gauld, 1973, 1976.

Ocellar-ocular interspace around 0.5 (female) to 1.0 times interocellar space (male); posterior ocellus to occipital carina 1.8 to 3.0 times maximum thickness of first flagellar segment, 0.8 to 2.0 times diameter of posterior ocellus; temple with maximum length just greater than, to 1.3 times greatest transverse diameter of eye and around 1.0 to 1.5 times length of first flagellar segment. Stemmaticum with complete sulci, stemmatico-ocular line often represented. Occipital carina squared or rounded centrally. Gena 0.4 to 1.0 times width of mandible base; postgena around 4.0, to nearly 6.0 times length of genal inflection, latter 0.3 to 0.4 times width of mandible base. Facioclypeal area transverse; mandible with rectangular to obtuse gape, distinct internal angles to the teeth, the flange indistinctly punctured medially. Epistomal punctures tending to be closer than those of orbits; last two segments of maxillary palpus unequal. First flagellar segment distinctly over 3.0, to around 4.0 times longer than broad. Flagellum with 48 to 56 segments in sample studied.

Thorax with moderate puncturation; mesonotum sometimes with trace of yellow "vittae"; abdomen sometimes black apically (female). Pleurosternal angle of epicnemium more or less rectangular, nearly aligned with sternal angles; lower sector of pleural epicnemium 0.5 to 0.6 times upper; scutellum with distinct lateral carinae.

Submedian cell of forewing with evenly distributed setae; substigmal speculum not extending beneath prestigma. Forewing 12—15 mm.

Hind femur relatively stout, trochantellus shorter than its minimum width in dorsal view. Tibial spinules quite strong. Mid tibial spurs of moderately unequal length.

Propodeum tending towards complete areolation.

Position of membrane of petiolar segment somewhat variable.

Variation. — It is difficult to assess fully the range in variation of this species, due to the small amount of material available for study. Sexual dimorphism seems considerable for head

characters, the lower limits for dimensions belonging more to the female than the male end of the range observed. The female may have the apical abdominal tergites determinately black. Characters quoted by Gauld (1978) relating to venational differences between *longigena* and *brevicornis* are unreliable in practice. I am also not satisfied that Gauld's use of the form of the front tarsus is not subject to overlap (in any case, a wide overlap does exist with another species not recognised by Gauld).

Remarks. — The name *costatus* Ratzeburg has been used for this species (Perkins, MS; Gauld, 1973, 1976) and was suggested as a possible synonym by Morley (1915). Interpretation of the name *costatus* Ratzeburg is discussed elsewhere in the present study.

Biology. — The few available rearing records for this species are from *Cucullia* (Noctuidae). The parasites are on the wing in early summer, during which time the host larvae are presumably in early instar. The species is excessively rare in occurrence, perhaps of southern distribution only in Britain.

Material examined. — 1 ♂, Spurn (VC61), 14.vii.1952 (W. D. Hincks) (MU); 1 ♂, Priors Marston, Warwicks. 26.vi.1943 (D. Allen) (MU); 1 ♀, Isle of Wight, Freshwater, ? iii.1971 (MU); ♂, no locality data, "? 11.vi.1944, ex *C. chamonillae* of 1942" (Sir L. Wakely) (BMNH); 2 ♂, "Colchester, Harwood" (BMNH): ♂, ex Harwood coll., no data (BMNH): ♂, Woodwalton Fen, Hunts., vii.1923 (P. Harwood) (BMNH); ♂, Corfe Castle, Dorset, 4.vii.1901, ex *C. chamonillae* (Bankes coll.) (BMNH); ♀, "S wold, 20.vii.01" (C. Morley) (BMNH).

Ophion brevicornis Morley
(figs. 28, 29)

Ophion brevicornis Morley, 1915: 274 (holotype, London). Gauld, 1976, 1978 (in part). Oosterbroek, 1978 (not examined).

Ophion costatus Ratzeburg; Brauns, Perkins, 19-- (MS) (in part).

Ophion "species X" Gauld, 1978 (in part).

Ocellar-ocular interspace 0.4 (female) to about 0.6 (male) times interocellar space; posterior ocellus to occipital carina 1.3 to 1.6 times maximum width of first flagellar segment; distinctly less than, to 1.4 times diameter of posterior ocellus. Maximum length of temple just shorter than greatest transverse diameter of eye (female) — about equal in male; temple 1.25—1.5 times length of first flagellar segment. Sulci

of stemmaticum — posteriors very deep and broad, laterals weak to moderate; stemmatico-occular line represented by zone of rough sculpture over a groove like depression. Occipital carina angled centrally (may be triangulate). Gena 0.5 to 0.8 times width of mandible base; postgena from shorter than (female) to nearly twice length of genal inflection (male). Latter 0.6 to 0.7 times width of mandible base. Facio-clypeal area strongly transverse; mandible rectangular to obtuse in gape, internal angles sharp, flange with a few minute punctures only. Epistoma and orbits with similar puncturation; last two segments of maxillary palpus strongly unequal. First flagellar segment distinctly less than 3.5 times longer than maximum width. Flagellum with 45 to 50 segments (small sample!).

Thorax rather closely punctured, with variable microsculpture; rather dark testaceous in colour; position of epicnemial angles rather variable, lower sector of pleural epicnemium 0.5 to more than 0.6 times upper. Scutellum not, or weakly carinate laterally.

Submedian cell of forewing with trichia evenly distributed; substigmal speculum not extending beneath prestigma; radius weakly, or not sinuate towards base. Fore wing: 10.5—13 mm in length.

Hind femur short and stout, trochantellus shorter than its minimum width in dorsal view; tibial spinules weak or moderate; mid tibial spurs of moderately unequal length.

Propodeum tending towards complete areolation, but lateral carina may be absent and superomedia incomplete.

Membrane of petiolar segment approximately opposite line of spiracles.

Variation. — Without a larger material, it is difficult to assess infraspecific variation.

Remarks. — The male paratype referred to by Gauld (1976) is a specimen of *O. perkinsi*.

J. F. Perkins placed *brevicornis* as a probable synonym of *longigena* Ths. (MS, and in BMNH collection), but this has been rejected by Gauld (1976, 1978). See also remarks under *longigena*.

Oosterbroek (1978) places the present species close to *parvulus* Kr., but has clearly not had the opportunity to compare other *longigena* group material. From that author's observations, *brevicornis* would appear to be commoner in Holland than it is in Britain.

Biology. — Oosterbroek (loc. cit.) cites *Cosmia trapezina* (Linnaeus) as a host. From the few British records of capture, a Noctuid host

maturing in early summer would seem to be a likely target. If *Cosmia* is the usual host, then this may be a good biological distinction from *longigena* Ths.

Material examined. — 2 ♀, Pinner, Middlesex, garden M.V. trap, vi.1977 (BK, private coll.); 1 ♂, Wenlock Edge, Shropshire, 24.vi.1958 (J. F. Perkins) (BMNH); 3 ♀, Colchester, at light, 1—3.vii.1936 (C. B. Williams) (BMNH); ♀, no data (Harwood) (BMNH); ♂, ♀, Höör District, Sweden, 17—21.vi.1938 (J. F. Perkins) (BMNH); ♂, Ideford, "Eng. 3", 21.vi.1942 (J. F. Perkins) (BMNH); 2 ♀, no data (BMNH); ♀, Darenth, Kent (coll. Champion) (BMNH); 2 ♀, Minstead, New Forest, Hants., 21—31.vii.1963 (L. W. Siggs) (BMNH). The Morley type female was taken at Bentley Woods, Suffolk, 23.vi.1899, by E. Platten (see Gauld, 1976) (BMNH). Just prior to completion of this work, J. Aubert sent me two additional specimens: 1 ♂, Ideford, 7.vi.1942 (J. F. Perkins); 1 ♀, Maujolia Neucliatie, 22.vi.1947 (J. Aubert) (see *O. crassicornis*).

Ophion perkinsi spec. nov.
(figs. 31, 32)

Ophion brevicornis Morley, 1915 (in part). Gauld, 1976 (in part).
Ophion "species X" Perkins, 19-- (MS).

Ocellar-ocular interspace 0.4 to 0.8 times interocellar space; posterior ocellus to occipital carina 1.5 to 2.0 times maximum width of first flagellar segment, just less than, to about 1.25 times the diameter of a posterior ocellus; maximum length of temple less than greatest transverse diameter of eye; same dimension a little less to a little more than length of first segment of flagellum. Lateral sulci of stemmaticum weak to absent, stemmatico-ocular line weak to quite deeply impressed. Occipital carina distinctly angled centrally. Gena 0.35—0.5 (female), up to 1.0 times width of mandible base (male). Postgena 0.8 to nearly 2.0 times length of genal inflection, latter less than 0.5 to 0.65 times width of mandible base. Facioclypeal area distinctly transverse; mandible with rectangular to obtuse gape, distinct internal angles to teeth, flange with indistinct medial punctures only. Punctures of epistoma and orbits of variable distribution; last two segments of maxillary palpus distinctly unequal; first segment of flagellum around 4.0, to about 5.0 times longer than maximum width. Flagellum with 45 to 50 segments, the central ones elongate.

Thorax with close puncturation, with noticeable microsculpture on pleura. Epicnemial angles not opposed, the sterno-pleural angle sharp and more or less rectangular. Lower sector of pleural epicnemium tending to be around 0.5 times upper sector. Scutellum with prominent lateral carinae.

Submedian cell of forewing with trichiae tending to be more closely spaced on lower third of cell than above this area; substigmal speculum not clearly extending beneath prestigma; radius sinuate towards base. Forewing length: 10.5—12.5 mm.

Hind femur not slender, trochantellus shorter than its minimum width in dorsal view. Tibial spinules not strong. Mid tibial spurs distinctly unequal in length.

Propodeum with carina lateralis and area superomedia tending to be complete, external dentiparal carinae obsolete.

Membrane of petiolar segment far behind line of the spiracles. Abdomen tending to be darkened ventrally.

Variation. — It is likely that when more material is seen, some extension may be required to the range of variation given here. In the key, I have attempted to stress characters which have been found stable within reasonable limits in other species groups where more material has been available for analysis. For this reason, some differences between species in the *longigena* group which may be quite reliable, have been omitted from the key. A darkening of the abdomen (both ventrally and apically) was the only really conspicuous component of variation found in some specimens of *perkinsi*.

Remarks. — This species was discovered by Perkins and is the "sp. X" of his manuscript key to *Ophion*. He placed his "sp. X" with *slaviceki* (see *luteus* L.) and distinguished the species on characters which in reality, mostly lie within the variation of *luteus* L. For several years, I had two specimens of *perkinsi* placed as indet. nr. *brevicornis* Morley. Eventually, I was able to align these with material placed separately by Perkins in the BM collections; although these specimens were not labelled as such, it seemed that they must be the material upon which Perkins had based his "sp. X". Since that date, these specimens have been amalgamated with "*slaviceki*" in the national collection; they were recently reinstated by the present author (1978).

Ophion perkinsi is not represented in the key given by Gauld (1978), nor by Oosterbroek

(1978) in his study of the Dutch species. The scutellar carinae and short hind trochantellus width generally distinguish it from forms of *luteus* with more buccate head; the antennal structure will separate *perkinsi* from *brevicornis*, to which latter species it is obviously closely related.

Biology. — Nothing is known regarding host preferences of the present species. Habitats frequented by it are as diverse as deciduous woodland and fen country. Its British distribution extends into Scotland, but it is rarely collected. The species flies during early summer.

Material examined. — Holotype ♀, Clandon, 5.vii.1953 (D. M. S. & J. F. Perkins) (BMNH); Paratypes, 1 ♀, West Suffolk, 1920 (P. Harwood) (BMNH); 3 ♀, Woodwalton, Hunts., vii.1923 (P. Harwood) (BMNH); 2 ♂, Woodwalton, Hunts., vii.1923 (P. Harwood) (BMNH); 1 ♂, Dartmoor, 26.viii.1935 (R. C. L. Perkins); 1 ♂, Killin, Perthshire, 22—30.vi.1932 (R. B. Benson) (BMNH); 1 ♂, Wytham Wood, Berks, 3.vii.1968, M.V. trap (BK); 1 ♂, Sandyhills, Lanarks., 23.viii.1966 (K. Stewart) (BK). As already stated, the Morley male paratype of *brevicornis* is a specimen of the present species (Surrey, 1900, coll. Sparke) (BMNH).

Ophion pteridis Kriechbaumer
(figs. 33—38a, graphs 6, 6a, 9)

Ophion pteridis Kriechbaumer, 1879 (lectotype female, Munich). Perkins, 19-- (MS). Gauld, 1976, 1978. Oosterbroek, 1978.
Ophion scutellaris Thomson; Morley, 1915 (misidentification).
Ophion pteridis Brauns; Gauld, 1973 (lapsus).

Ocellar-ocular interspace absent, to (exceptionally) 0.3 times interocellar space; posterior ocellus to occipital carina 1.2—1.5 times maximum width of first flagellar segment, 0.5—0.85 times diameter of a posterior ocellus. Temple much shorter than greatest transverse diameter of eye, at least marginally shorter than first flagellar segment. Sulci of stemmaticum complete, posterior sulcus tending to run into back of eye, lateral sulcus strong (usually deeper than mid-dorsal sulcus). Occipital carina usually squared, rounded or dipped (sometimes clearly angled) centrally. Gena less than 0.3 to (some males) 0.7 times width of mandible base; postgena usually less than or equal to length of genal inflection, latter 0.7—0.8 times width of mandible base. Eyes somewhat convergent beneath in frontal

view; facioclypeal area subquadrate to higher than broad; mandible not long, gape rectangular to obtuse, internal angles sharp, flange largely impunctate. Punctures of epistoma and orbits of similar distribution; last two segments of maxillary palpus unequal; dorsal edge of mandible about same width as a tooth, rounded into front of mandible. First flagellar segment 3.5 (exceptionally only 3.0) to over 4.0 times longer than broad. Flagellum with usual range of 53—57 segments (mean around 55): exceptionally, up to 59 present.

Thorax with distinct coriaceous microsculpture between punctures (especially on mesopleura); colour rather reddish; epicnemial angles not aligned, pleurosternal angle sharp, more or less rectangular, lower sector of pleural epicnemium usually less than or equal to 0.5 times upper. Scutellum usually carinate.

Submedian cell with sparse, elongate, evenly distributed trichiae. Substigmal speculum not extending beneath prestigma, trichiae in latter region unusually elongate. Radius sinuate towards base. Length 10—17 mm.

Hind femur quite slender, trochantellus shorter than its minimum width in dorsal view. Tibial spinules weak. Mid tibial spurs of unequal length (both elongate).

Propodeum with carina lateralis; superomedia and petiolar carinae rarely complete.

Membrane of petiolar segment well behind line of spiracles.

Variation. — Males overlapping with the *luteus* group with respect to the ocellar-ocular interspace are not uncommon. The scutellar carinae also, are frequently weak or absent. There is also variation in the development of the propodeal carinae, which may range from considerable reduction to a condition of nearly complete areolation; specimens approaching the latter extreme are rare. Again, the darker colouration and rougher microsculpture which tend to distinguish this from the next species, are subject to quite frequent exception. Where difficulty is experienced in separating variants of *pteridis* and *parvulus* (or *luteus* from the former), a point by point comparison with the descriptions (bearing in mind the given variation) will generally produce a satisfactory result. I do not find that Gauld (1978) has allowed sufficiently for infraspecific variation in attempting to distinguish *pteridis* and *parvulus*.

Remarks. — Perkins' views on the identity of this species have been confirmed with reference to the type. In his original description, Kriechbaumer refers to a conspicuous dark and light patterning, a feature absent in most specimens I have studied — but certainly evident in the type. I have seen a few British specimens which do have this colouration, which I suspect is an artefact produced either by a killing agent or by decay of internal tissues.

Biology. — *O. pteridis* has been reared quite regularly through night feeding Noctuid larvae on seed pods of *Campanula* (*Hadena*). Other, possibly regular hosts include *Ceramica pisi* (Linnaeus) and *Diataraxia oleracea* (Linnaeus). These all pass the winter in the pupa state, and for the most part, are not arboreal in habit. They are apparently fairly mature larvae during the flight period of the parasites.

Material examined. — Lectotype ♀ (Munich); 7 ♂, 50 ♀, Minstead, New Forest, Hants., M.V. trap, vii.—ix.1963—1975 (Siggs) (BMNH); 1 ♂, 1 ♀, Tiverton, vii.-ix.1954 (F. H. Lyon) (BMNH); 1 ♂, Eltham, Surrey, 30.vii.1892 (MU); 1 ♂, Ogden Clough, Lancs., ex *M. pisi*, host 13.ix.1936, emerged 30.v.1937 (A. Brindle) (MU); 1 ♀, Timperley, Cheshire, 1.ix.1930 (H. R. Collett) (MU); 1 ♀, Hale, Cheshire, 20.viii.1932 (H. R. Collett) (MU); 1 ♀, Framdley House, Cheshire, 3.ix.1946 (A. W. Boyd) (MU); "Lichfield, Carr" (MU); 1 ♂, Burnley, Lancs., 26.v.1923 (W. H. Clutten) (MU); 1 ♂, Staley, Cheshire, 14.viii.1945 (H. N. Michaelis) (MU); 1 ♂, Burnley, Lancs., 27.v.1923 (W. G. Clutten) (MU); 1 ♀, Southport, 18.v.1929 (W. G. Clutten) (MU); 1 ♂, Solihull, Birmingham, 17.viii.1969, M.V. trap (M. R. Shaw) (BK); 1 ♂, Speke, Liverpool, 12.viii.1972 (BK); Marston, Oxford, 9.viii.1970 (BK); 1 ♂, Weymouth, Dorset, 16.viii.1974 (M. J. Smith) (BK); 1 ♂, Richmond, Surrey, 31.vii.1971 (BK); 3 ♀, Solihull, Birmingham, viii.1969, M.V. trap (M. R. Shaw) (BK); 1 ♀, Mugdock, Glasgow, 11.ix.1971 (BK); 1 ♀, Sandyhills, Lanarks., 23.viii.1966 (K. Stewart) (BK); 1 ♀, Lambhill, Glasgow, 8.ix.1974 (BK); 1 ♀, Possil Marsh, Glasgow, 4.ix.1971 (BK); 1 ♂, 1 ♀, Pinner, Middlesex, garden M.V. trap, vi.1977 (BK); 1 ♂, Claygate, Surrey, 2.viii.1958 (D. M. S. Perkins) (BMNH); 1 ♀, Southampton, at light, 28.viii.1954 (W. Tampion) (BMNH); 1 ♀, Crapstone, Devon, 30.viii.1968 (BMNH); 1 ♂, 1 ♀, Colthrop, 1906, ex *D. capsincola* (Lyle coll.) (BMNH); 3 ♂, Exebridge, NS., 15.viii.1958 (D. H. Harvey) (BMNH); 1 ♂, Digby, Lincs., at light, 18.viii.1958 (C. R.

Vardy) (BMNH); ? sex (damaged), Seaford, ex *D. cucubali*, emerged 3.vi.1943 (Sir L. Wakely) (BMNH); 1 ♂, Black Mountains, Powis, Wales, ex *Ceramica pisi*, host larva coll. 3.viii.1975, parasite emerged from prepupa, viii.1975, adult parasite, 23.vii.1976 (S. J. Hopton) (Shaw coll.); 1 ♂, Taunton, ex *C. pisi*, host larva 15.viii.1974, paras. larva emerged ? viii.1974, adult 26.vi.1975 (K. Noble) (Shaw coll.); 1 ♀, East Didsbury, Manchester, ex *D. oleracea*, host larva 15.ix.1974, adult paras. emerged 20.vii.1975 (M. R. Shaw); 1 ♂, 1 ♀, Chislehurst, Kent, ex *D. oleracea*, host larvae 15.x.1972, emerged 30.vi.1973, 5.vii.1973 (Shaw coll.); 1 ♂, 1 ♀, host larvae 26.vii.1973, parasite larva left host prepupa c.9.ix.1973, paras. adults 1.vi. & 13.vi.1974, ex *H. bicruris* (M. R. Shaw coll.); 1 ♂, Solihull, Warwicks., ex ? *Mamestra brassicae*, host coll. 28.viii.1973, paras. larva c.15.ix.1973, adult 18.vii.1974 (M. R. Shaw coll.); 1 ♂, 1 ♀, East Didsbury, Manchester, host 8.ix.1977, paras. larva 12.x.1977, adults 26.vii. & 9.viii.1978 (M. R. Shaw); ex *D. capsincola*, 1.vi.1902 (Morley) (BMNH).

Ophion parvulus Kriechbaumer
(figs. 38b—40, 41b—45, graphs 6, 6a, 8, 9)

Ophion parvulus Kriechbaumer, 1879 (lectotype male, Munich). Perkins, 19-- (MS: BMNH). Gauld, 1976, 1978. Oosterbroek, 1978.
Ophion "species Y" Perkins, 19-- (MS: Oxford).
Ophion parvulus Brauns; Gauld, 1973 (lapsus).

Ocellar-ocular interspace absent to 0.3 times interocellar space, longest in males; posterior ocellus to occipital carina 1.2—2.0 times maximum width of first flagellar segment, 0.65—0.8 times diameter of a posterior ocellus. Temple much shorter than eye, less than to distinctly longer than first flagellar segment. Posterior sulcus of stemmaticum tending to terminate at margin of eye, lateral sulcus weaker than mid-dorsal sulcus, frequently absent. Occipital carina usually rounded, squared or dipped centrally (though sometimes angled). Gena 0.3—0.75 times width of mandible base (longest in males); postgena usually longer than or equal to length of genal inflection, latter 0.35 to 0.7 times width of mandible base. Eyes more or less parallel in frontal view; facioclypeal area subquadrate to wider than high; mandible with rectangular to obtuse gape, sharp internal angles to the teeth, flange indistinctly punctured medially. Punctures of epistoma similar, to somewhat closer than those of orbits. Last two segments of max-

illary palpus unequal. Dorsal edge of mandible narrower than a tooth, sharply defined from front. First flagellar segment sometimes as short as 3.0 times, usually around 4.0 to 5.0 times longer than broad. Usual range of 47—53 flagellar segments (mean around 51); holotype with only 45 flagellars.

Thorax with moderate punctures, micro-sculpture rather weak throughout, colour testaceous, pleura often yellow marked above (mesonotum rarely with yellow "vittae"); epicnemial angles remote, to more or less in line; pleurosternal angle rounded, often distinctly obtuse. Lower sector of pleural epicnemium 0.5 to 0.8 times upper sector. Scutellum rarely with a trace of lateral carinae.

Submedian cell of forewing with trichiae short, often sparser dorsally than below. Substigmal speculum generally produced beneath prestigma. Radius evenly curved — to quite deeply sinuate towards base.

Hind femur quite slender, trochantellus shorter than minimum width in dorsal view; tibial spinules weak, spurs of mid tibia not elongate, of moderately unequal length.

Propodeum usually with carina lateralis about as strong as dorsal carinae; superomedia and petiolar carinae usually incomplete, though less so than in *pteridis*.

Membrane of petiolar segment subopposite spiracles.

Variation. — Forms with a distinct ocellar-ocular interspace are by no means rare, especially amongst males. These can readily be distinguished from *luteus* group species from the key. Care must be taken however, to avoid misidentification of yellow patterned individuals as *obscuratus*, since the mesonotum may be "vittate" and the stigmal apex yellow in exceptional specimens. Much greater difficulty will be experienced in separating *parvulus* variants with short first flagellar segment from *mocsaryi*, especially since the distribution of the trichiae on the submedian cell (Gauld, 1978) is unstable; in addition, the substigmal speculum to some extent, along with the carination of the propodeum, are subject to variation. Where difficulty is met, a point by point comparison of descriptions will usually produce an acceptable solution. Confusion with *pteridis* is also quite likely to occur, especially since there is a recurring form of *parvulus* with distinctly sinuate radius. When attempting to separate these from forms of *pteridis* which converge on *parvulus* (e.g., in

Graph 6. Temporal frequency distributions for *Ophion parvulus* Kriechb. and *O. pteridis* Kriechb.
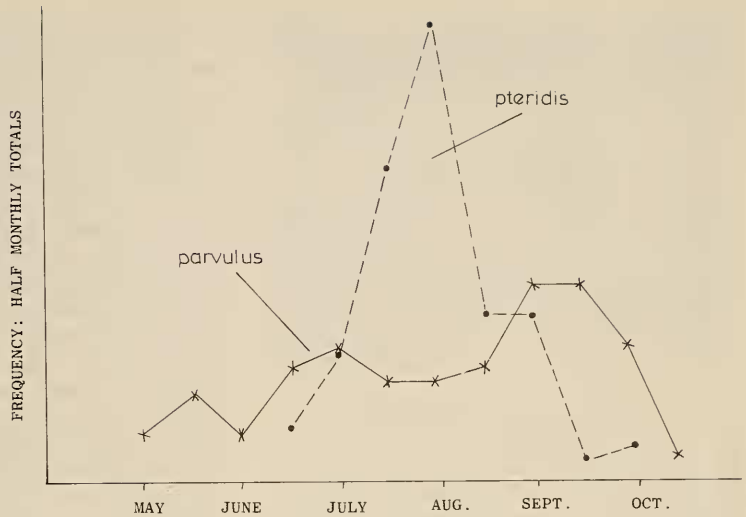
lack of scutellar carinae, etc.), special attention should be paid to the shape of the facioclypeal area, the longer postgena and temple of *parvulus* males and the position of the petiolar membrane.

Remarks. — Perkins originally referred to this species as "sp. Y" (MS), later suggesting the name *parvulus* Kr. I have confirmed this synonymy with reference to the type. The latter is an abnormally small specimen of the species and it lacks the darkened mesonotum mentioned by Kriechbaumer (1879). It is otherwise in agreement with the original description and with that given in the present study.

Biology. — Hosts are Noctuidae which overwinter as pupae. In early summer, *Orthosia* species seem to be selected, while the autumn brood has been reared through *Euplexia* and *Acronicta*. The biological significance of this apparent bivoltinism is unclear, since cocoons from spring *Orthosia* appear to produce parasite adults the following year (see remarks under *obscuratus*). As unusual characteristic is the habit of cocoon-forming within the ruptured pupal remains of the host.

Common and widespread, perhaps less frequent in the north.

Material examined. — Lectotype ♂ (Munich); 34 ♂, 41 ♀, Minstead, New Forest, Hants., M.V. trap, vi.—xi.1963—75 (L. W. Siggs) (BK) (BMNH); 3 ♀, Tiverton, vii.—ix.1954 (F. H. Lyon) (BMNH); 2 ♂, "O. Winch. Hill, S. Hants.", 4.viii.1954 (A. H. Sperring) (BMNH); 1 ♀, Manchester, ex *O. gothica*, 8.vi.1948 (L. Nathan) (MU); 1 ♂, Malham Tarn, 25.vii.1958 (W. D. Hincks) (MU); 1 ♀, Frandley Hs., Cheshire, 11.viii.1957 (Boyd) (MU); 1 ♀, Manchester, ex *gothica*, 2.vi.1945 (MU); 1 ♀, Doncaster, 14.vi.1921 (Clutten) (MU); 1 ♂, Keighley Dist., 28.vi.1945 (J. Wood) (MU); 1 ♂, Penrith, Cumbs., 18.vii.1953 (W. T. Davidson) (MU); 1 ♀, "Lichfield, Carr" (MU); 1 ♀, Delamere, Cheshire, 22.ix.1951 (H. N. Michaelis) (MU); 1 ♀, Burnley, ex *E. lucipara*, 2.vii.1918 (Clutten) (BMNH); 1 ♂, Chat Moss, Lancs., ex *A. leporina*, 1.viii.1937 (L. Nathan) (MU); 3 ♂, Devon, M.V. trap, 10.vii.1973 (M. R. Shaw) (BK); 1 ♂, Stevenston, Ayrshire, 15.viii.1965 (BK); 1 ♂, Milton Lockhart, Lanarks, vii.1965, ex coccoon under bark, probably *Acronicta* sp. (BK); 13 ♂, Wytham, Berks., M.V. trap, 3.vii.—22.ix.1968 (J. P. Brock, M. C. Birch, N. Rae-Jones) (BK); 2 ♂, "Oxford" (M. P. Hassel) (BK); 1 ♂, Cornwall 4—10.viii.1974 (J. St. E. Cardew) (BK); 1 ♂, Solihull, WKS., 18.7.1969 (M. R. Shaw) (BMNH); 1 ♂, Woodchester Park, Glos., ix.1972, M.V. trap (BK); 9 ♀, Wytham, Berks., 28.v.-22.ix.1966 (BK); 1 ♀, "Oxford" (M. P. Hassel) (BK); 1 ♂, 3 ♀, Pinner, Middx., garden M.V. trap, vi.1977 (BK, private coll.); 3 ♂, 1 ♀, Colchester, 1945 (Harwood) (BMNH); 2 ♀, Arkley, 13.ix.1954 (T. G. Howarth) (BMNH); 1 ♀, Giggleswick, Yorkshire, 21.viii.1964 (E. Burtt) (BMNH); 1 ♀, Killin, Perthshire, vi.1932 (K. G. Blair) (BMNH); 1 ♂, Old Winchester, Hants., 28.viii.1954 (A. H. Sperring) (BMNH); 1 ♀, Bramshaw Wood, New Forest, Hants., on birch, 20.vi.1964 (L. W. Siggs) (BMNH); 1 ♀,

Wimbledon, Surrey, 28.v.1957 (D. J. Clark) (BMNH); 1 ♂, Windsor Forest, Berks., v.1953 (H. Donisthorpe) (BMNH); 1 (damaged) Bentley, NE, ex *C. coryli* (Harwood) (BMNH).

Discussion of species criteria in the pteridis-parvulus species pair

A Mann-Whitney test on the frequency distributions of flagellar segment number in these two species shows significant median separation for each segregate: P < 0.001 (graphs 2, 6a). The bimodality of the *parvulus* curve (absent in *pteridis*) may reflect an underlying genetic difference which has not received notice.
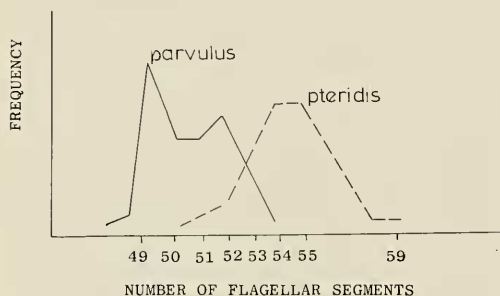
Graph 6a. Flagellar segments frequency distributions for *Ophion parvulus* Kriechb. and *O. pteridis* Kriechb.

The temporal distributions of *parvulus* and *pteridis* show a wide overlap, but *pteridis* is univoltine, *parvulus* bivoltine. Again, *pteridis* reaches a peak in numbers during the inter-generation depression of *parvulus* (graph 6).

From earlier remarks, it is clear that breeding experiments to determine the biological nature of bivoltinism in the last mentioned species would be very desirable. Ecological separation of *pteridis* and *parvulus* is decisive, but the latter could possibly conceal two biologically distinct, yet structurally identical species: circumstantial evidence from biometric analysis of similar phenomena in *obscuratus* however, seems to suggest that a single species can be a "facultative bivoltine" unit.

Ophion mocsaryi Brauns
(figs. 46—50a, graphs 7—9)

Ophion mocsaryi Brauns, 1889: 89 (holotype female, Budapest). Schmiedeknecht, 1908. Morley, 1915. Perkins, 19-- (MS) (in part). Gauld, 1973, 1976, 1978 (in part). Oosterbroek, 1978.

Ocellar-ocular interspace absent, or very short; posterior ocellus to occipital carina usual-

ly more than, sometimes equal to maximum width of first flagellar segment, at least 0.5 and *usually* around 0.7 times diameter of a posterior ocellus; ocellar interspace greater than or equal to maximum width of first flagellar segment. Temple far shorter than eye, 1.0 to 1.25 times length of first flagellar segment. Posterior sulcus of stemmaticum deeply impressed, ending at eye; lateral sulci of stemmaticum weakly developed. Vertex with occipital carina sharply angled centrally. Gena 0.2 to nearly 0.4 times width of mandible base; postgena distinctly less, to distinctly greater than length of genal inflection. Latter around two thirds of width of mandible base. Facioclypeal area subquadrate; mandible with rectangular to obtuse gape, sharp internal angles, largely impunctate flange. Epistomal and orbital puncturation similar. Last two segments of maxillary palpus slightly to strongly unequal in length. Dorsal edge of mandible as wide as a tooth, sharply offset from front. First flagellar segment 2.4 to 3.5 times longer than maximum width. Flagellum with range of 50 to 58 segments (mean about 54). Thorax moderately punctured, testaceous. Pleurosternal angle of epicnemium sharp, often rectangular, nearly aligned with sternal angles. Lower sector of pleural epicnemium less than, to equal to 0.6 times upper sector. Scutellum not carinate.

Forewing with submedian cell having short, evenly spaced trichiation. Nervellus broken at or below the centre. Substigmal speculum not produced into area beneath prestigma, that area with short trichiae. Radius weakly to strongly sinuate towards base. Forewing: 11.5—15.5 mm.

Hind femur moderately slender, trochantellus shorter than minimum width. Tibial spinules moderate. Mid tibial spurs unequal.

Propodeum usually lacking distinct carina lateralis, dorsal carinae often complete and strongly raised; spiracle more ovoid.

Membrane of petiolar segment approximately in line with the spiracles.

Variation. — This species has generally been characterised by authors, through the presence of a complete area superomedia on the propodeum. This is not always in evidence, but is nevertheless more frequently strongly developed than in the majority of specimens of *pteridis* or *parvulus*. Some variants of *mocsaryi* are liable to be confused with *parvulus* and difficulty will also be experienced in separating the present from

the next species. These problems are discussed fully under *parvulus* and *costatus*.

Remarks. — Specimens identified as *mocsaryi* in collections will generally be found to include material of *costatus* Ratzeburg. These were not distinguished by Perkins, either in his manuscript key, nor in the British Museum collections. The type of *mocsaryi* has been seen and the interpretation of authors confirmed.

Gauld (1978) does not allow for infraspecific variation in attempting to distinguish the *mocsaryi — costatus* species pair from the related *pteridis — parvulus* pair. Females are particularly likely to overlap on characters relating to the tenth flagellar segment, as defined by that author. The characters used by Oosterbroek (1978), partially after Gauld, are likewise unreliable for separation of species in the *mocsaryi* group.

Biology. — This species has been reared through night feeding Noctuid larvae maturing during early summer on low shrubs. These include *Triphaena* and *Orthosiinae*. *Ophion mocsaryi* is widely distributed and sporadically common in Britain, possibly more rare in Scotland (no records as yet).

Material examined. — Holotype ♀, Budapest, 1879, ex *Cosmia ambusta* (Prague); Paratype 1 ♂, 1 ♀, same data as holotype, ♂, "19.ii.1879", ♀, "19.iii.1879" (Berlin); 21 ♂, Stark Ponds, Kingsteynton, 24.v.—8.vi.1942 (J. F. Perkins) (BMNH); 6 ♂, 21 ♀, Minstead, New Forest, Hants., M.V. trap, 18.v.—26.vii.1963—4—5 (L. W. Siggs) (BMNH); 1 ♂, 1 ♀, Minstead, New Forest, M.V., 25.v. & 26.v.1975 (Siggs) (BK); 1 ♂, Formby Point, Lancs., ex *T. fimbria*, host 16.xi.1950, parasite emerged 16.iv.1951 (K. C. Greenwood) (MU); 2 ♂, "Lichfield, Carr, 1920" (MU); 1 ♂, Freshfield, Lancs., 10.vi.1957 (W. D. Hincks) (MU); ? sex (damaged): Middlewood, Cheshire, 6.vi.1920 (H. Britten) (MU); 1 ♂, Formby Moss, Lancs., ex *T. fimbria*, host 17.xi.1950, emerged 23.iv.1951 (K. C. Greenwood) (MU); 1 ♀, Ainsdale, Lancs., swept from *Salix repens* at night, 25.vi.1974 (M. R. Shaw) (BK); 1 ♀, Wytham, Berks., M.V. trap, vii.1968 (M. C. Birch) (BK); 2 ♀, Wytham, Berks., M.V., 9.vi.1969, 27.vi.1968 (BK); 2 ♀, "Oxford" (M. P. Hassel) (BK); 1 ♂, Minstead, New Forest, M.V., 28.v.1976 (L. W. Siggs) (BK); 1 ♂, Newton Abbot, SD., 1.vi.1941 (J. F. Perkins) (BMNH); 1 ♀, Tiverton, ND., vi.1955 (F. H. Lyon) (BMNH); 4 ♂, Starks Ponds, King's

Steynton, 24.v.—8.vi.1941 (J. F. Perkins) (BMNH); 2 ♀, Minstead, New Forest, M.V., 9.vi.1962 (L. W. Siggs) (BMNH); 1 ♀, Monk's Soham, Suffolk, with coccoon, 4.vi.1909 (Morley) (BMNH); 1 ♂, Ainsdale, Lancs., ex ? *Xanthia icteritia* on *Salix repens*, host larva coll. 5.vi.1975, parasite larva from host prepupa vi.75, paras. adult 11.iv.1976 (M. R. Shaw coll.); 1 ♀, Ainsdale, Lancs., ex *Agrochola* or *Xanthia* sp., host larva on *S. repens* 5.vi.1975, parasite larva from host prepupa 16.vi.75, adult emerged 15.v.1976 (M. R. Shaw coll.); damaged specimen — St. Annes', 1910, ex *Orthosia lota* (Clutten) (BMNH).

Ophion costatus Ratzeburg
(figs. 50b—52, graphs 7—9)

Ophion costatus Ratzeburg, 1848: 79 (holotype destroyed). Schmiedeknecht, 1908: 1438. Gauld, 1978. Oosterbroek, 1978.
Ophion mocsaryi Brauns; Perkins, 19-- (MS) (in part). Gauld, 1978 (in part).

Ocellar-ocular interspace absent, or very short; posterior ocellus to occipital carina less than or equal to maximum width of first flagellar segment, less than 0.5, to 0.7 times diameter of posterior ocellus; ocellar interspace most usually narrower than maximum width of first segment of flagellum. Temple much shorter than eye, 0.9 to 1.25 times length of first flagellar segment. Posterior sulcus of stemmaticum forming very deep grooves behind posterior ocelli, ending at eye; lateral sulcus weak. Occipital carina with rounded, weak angulation centrally. Gena around 0.2 to nearly 0.4 times width of mandible base; postgena distinctly less, to distinctly greater than length of genal inflection — latter about two thirds width of mandible base. Facioclypeal area subquadrate. Mandible as in *mocsaryi*. Epistoma and orbits with fine puncturation. Last segment of maxillary palpus of same length, or slightly longer than penultimate segment. First flagellar segment 2.3 to nearly 3.0 times longer than maximum width (shorter and broader on average than in *mocsaryi*). Flagellum with usual range: 56 to 63 segments (mean about 61).

Thorax moderately punctured, tending towards darker, more reddish testaceous. Pleurosternal angle of epicnemium sharp, not obtuse — more or less aligned with sternal angles; lower sector of pleural epicnemiun around 0.6 × upper sector. Scutellum not carinate.

Wings similar to *mocsaryi*, but hind wing with the nervellus intercepted *above* centre in

about 30% of specimens. Forewing: 14—17 mm.

Leg characters as in *mocsaryi*.

Propodeum often lacking distinct carina lateralis, the dorsal carinae frequently complete and often very strongly raised; propodeal spiracle more linear than in *mocsaryi*.

Abdomen as in *mocsaryi*.

Variation. — Due to overlap with the preceding species with regard to the number of flagellar segments and the interception of the nervellus, it is likely that difficulty will be met with in attempting to separate the present species from *mocsaryi*. For this reason, *all* other characters must be examined for reliable identification of *costatus*.

Remarks. — The history of this species is somewhat tortuous and can perhaps be summarised as follows:

(1) The original description of *costatus* Ratzeburg could apply to more than one species of *Ophion*.

(2) The holotype of *costatus* no longer exists.

(3) Perkins used the name *costatus* for *longigena* Ths. on the basis of his study of the Brauns collection, since Brauns (1889) was first reviser of *costatus* Ratz. (Perkins, pers. comm., 1978).

(4) Brauns himself doubted whether his own species was the same as that described by Ratzeburg. Furthermore, there now exists no material of *costatus* Ratz.-Brauns in the Brauns collection.

(5) Schmiedeknecht (1908) identified *costatus* Ratz. as a form close to *mocsaryi* Brauns, differing in characters which could only refer to variants of the species for which I have adopted the name *costatus* Ratz.

(6) Gauld (1973) published the Perkins use of *costatus* (i.e., for *longigena* Ths.).

(7) Gauld (1978) now uses the name *costatus* in the same context as did Schmiedeknecht, without comment as to his change of opinion on the Perkins interpretation. The characters given by Gauld for separation of *costatus* and *mocsaryi* follow the Schmiedeknecht diagnosis for the most part, and will only separate about 30% of material.

It will be found, in some British collections, that the present species has quite often been misidentified as *longicornis* Brauns (see *scutellaris* Thomson). Post-1974, a number of specimens in the British Museum and Manchester Museum collections had been identified as *costatus* Ratzeburg, by the present author.

Biology. — Ratzeburg's type of *costatus* was reared through *Acronicta aceris* (Linnaeus). I have come across no further material reared through this host, for any *Ophion* species. M. R. Shaw has reared *costatus* (as here recognised) through *Cucullia* (Noctuidae). The host range may then include both arboreal and other Noctuid larvae which pass the winter in the pupa stage. The true identity of Ratzeburg's species however, remains uncertain.

The species is seldom taken in any numbers, but is widely distributed in England. As yet, there are no Scottish records.
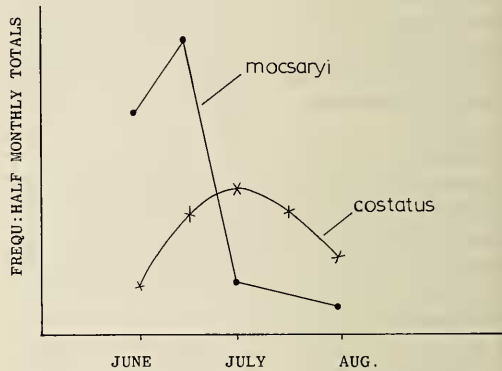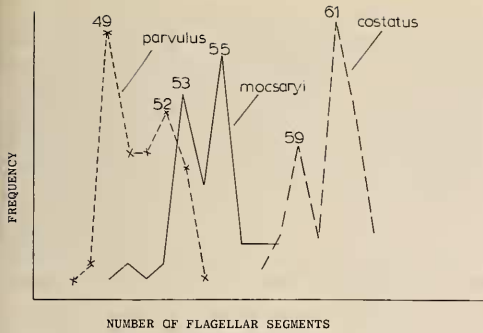

Graph 7. Temporal frequency distributions for *Ophion mocsaryi* Brauns and *O. costatus* Ratzeburg.

Material examined. — 6 ♂, Minstead, New Forest, Hants., M.V. trap 31.v.1964, 4.vi.1964, 25.vi.1963, 25.vi.1965, 8.vi.1965, 2 ♀, same data, 4.vi.1964, 7.vii.1964 (L. W. Siggs) (BMNH); 1 ♂, Hale, Cheshire, 16.vii.1923 (H. R. P. Collett) (MU); 1 ♂, 1 ♀, Timperley, Cheshire, 23.vii.1932 (H. R. P. Collett) (MU); 7 ♂, 3 ♀, Wytham Wood, Berks., M.V. trap, 4.vi.-12.vii.1968, 6.vi.1967; 2.vi.1969, 22.vi-.1971 (J. P. Brock, M. C. Birch, M. R. Shaw) (BK); 2 ♀, Woodchester Park, Glos., 7.vii.1973 (M. R. Shaw); 2 ♂, Hereford, Craswall, 23—24.vi.1973 (BMNH); 1 ♂, Reichenau district, Semmeringgebiet, Lower Austria, 26.v.1957 (R. B. Benson) (BMNH); 1 ♀, Oxford, ex *Cucullia verbasci*, host coll. 3.vii.1970, parasite adult emerged: 28.v.1971 (M. R. Shaw collection); 2 ♂, Kirton, Suffolk, viii.1979 (M. J. Smith).

Discussion of species criteria in the **mocsaryi — costatus** species pair

A Mann-Whitney analysis for comparison of frequency distributions of flagellar segment number showed significant separation; SND =

Graph 8. Flagellar segments frequency distributions for *Ophion parvulus* Kriechb., *O. mocsaryi* Brauns and *O. costatus* Ratzeburg.

7.03; P < 0.001 (see graph 8). A curve combining the two species is quadrimodal, preserving the sexual bimodality apparent in the individual distributions, plus the overall bimodality of the species segregates.

In terms of overall resemblance, these two species are closer than any other species pair in *Ophion*. However, the actual zone of overlap in flagellar segment number is distinctly less than that found in *parvulus/pteridis* (compare graphs 6a and 8). Furthermore, the overall range for this same character in a combined *mocsaryi — costatus* aggregate is of even greater magnitude than a similar combination of *pteridis — parvulus* composition. The possibility of one extremely variable species may perhaps be ruled out on the absence of any threshold effect in the regression curve (graph 5), as was observed for the polymorphic *obscuratus*. On the other hand, *costatus* is very nearly an extension of the *mocsaryi* curve on a simple linear basis. The rather small sample size for *costatus* inevitably makes for difficulty in arriving at an absolutely final assessment of the said data.
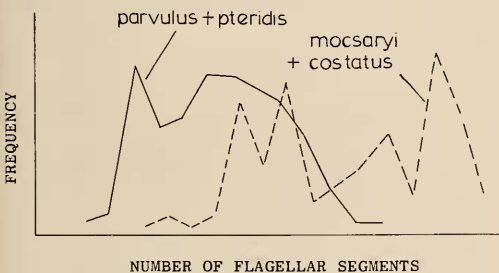
Graph 9. Combined flagellar segments frequency distributions for *Ophion parvulus/pteridis* and *O. mocsaryi/costatus*.

Coming now to the question of the temporal frequency distributions of the two species in question (see graph 7), it is found that *costatus* tends to be on the increase during the late decline in *mocsaryi* numbers. This fits well with the phasing of the host larvae, those of the first species deriving from early summer moths, at a time when *mocsaryi* hosts are mature larvae. From the rather male dominated sex ratio in *costatus*, it could be supposed that this was really a male trend from *mocsaryi* — but these males would be appearing in the population at the same time as the female sex was disappearing! This seems biologically unlikely, and the apparent predominance of males in *costatus* could be an effect of small sample size: I have also seen material obviously drawn from a heavily male dominated population of "normal" *mocsaryi*. In solving this anomaly, I have drawn particularly on the extremely valuable material collected at Minstead, New Forest on a year by year basis, by the late L. W. Siggs.

A final comment on the possibility of a host correlated dimorphism underlying the *costatus-mocsaryi* species pair comes from the fact that *mocsaryi* specimens reared through the large Noctuid *Noctua* do not converge on *costatus* form, as compared to the *Orthosiinae* rearings.

O. mocsaryi and *costatus* remain the most closely related species pair amongst British *Ophion* species. Investigations concerned with establishing whether or not these segregates are really biologically distinct should not only deal with a larger and more widely distributed set of population samples, but must also bear in mind the probable biological criteria already discussed. It is particularly important that the definition of segregates given herein be taken fully into account, in respect of apparent intermediate forms. The characters given by Gauld (loc. cit.) certainly break down with an examination of infraspecific variation, even with the relatively small sample sizes already available. It perhaps goes without saying, that breeding experiments are much to be desired in resolving outstanding problems.

SUMMARY OF HOST SPECIES FOR *OPHION*
(VERIFIED RECORDS ONLY)

minutus
  Agriopis (*Erannis* auctt., ptm.)
  A. aurantiaria (Hubn.)
  A. marginaria (F.) (prob. plus *E. defoliaria*)
ventricosus

Apocheima pilosaria (D. & S.) (*Phigalia pedaria* F. of auctt.)
scutellaris
   Lycophotia porphyrea (D. & S.) (*L. varia*, of auctt.)
   Noctua (*Triphaena*, auctt.) *fimbriata* (Schreber)
   Xestia (*Amathes*, auctt.) *xanthographa* (Schiff.)
   Aporophyla nigra (Haw.)
luteus
   Ochropleura (*Agrotis*, auctt.) *praecox* (L.)
   (usual host not known)
obscuratus
   Acronicta cuspis (Hubn.)
   Lycophotia porphyrea (D. & S.)
   Noctua (*Triphaena*, auctt.) *comes* (Hubn.)
   N. fimbriata (Schreber)
   N. interjecta (Hubn.)
   Mythimna impura (Hubn.) (formerly *Leucania*)
   M. ferrago (F.)
   Xestia (*Amathes*, auctt.) *agathina* (Duponch.)
   X. castanea (Esper)
   X. baja (Schiff.)
   Graphiphora augur (F.).
   Agrochola or *Xanthia* sp. indet.
forticornis
   Ochropleura (*Agrotis*, auctt.) *praecox* (L.)
longigena
   Cucullia chamomillae (Schiff.)
   C. ?*scrophulariae* (Capieux)
brevicornis
   Cosmia trapezina (L.)
perkinsi
   unknown
crassicornis
   Aporophyla nigra (Haw.)
parvulus
   Orthosia cruda (Schiff.)
   O. gothica (L.)
   Euplexia lucipara (L.)
   Acronicta leporina (L.)
   Acronicta sp. indet.
   Ipimorpha retusa (L.)
   Cosmia trapezina (L.)
   Colocasia coryli (L.)
pteridis
   Ceramica pisi (L.)
   Hadena bicruris (Hufn.)
   H. rivularis (F.)
   Diataraxia oleracea (L.)
   ?*Apamea unanimis* (Hubn.)
mocsaryi
   Agrochola lota (Clerck)
   Noctua (*Triphaena*, auctt.) *fimbriata* (Schreber)
   Atethmia ambusta (F.)
   Xanthia or *Agrochola* sp. indet.
costatus
   Acronicta aceris (L.) . . . lost type!
   Cucullia verbasci (L.)

Conclusions

Comparative studies show much infraspecific variation in *Ophion* species, which may greatly overstep species-to-species differentials (see curve 2, for example). Members of the *luteus* complex are extremely closely related and difficult to define, other than in a context of highly polythetic character distribution. The question of temporal speciation cannot be ruled out for *obscuratus* and *parvulus*, nor is it yet entirely certain that *mocsaryi* and *costatus* are real biological species isolates. Breeding experiments with the last two forms (also with *luteus*, *obscuratus* and *parvulus*) will be necessary in order to fully resolve some of the questions which cannot be fully answered through morphological investigations alone.

Appendix: Notes on *Platophion*

Platophion species are at once recognisable through their lack of any occipital carina; they appear to be parasites of Thyatiridae (BMNH records, confirmed M. R. Shaw, pers. comm.). Both generic and species diagnoses have been affected by the small number of available specimens. Preliminary study suggests that the two species can be distinguished thus:
ocellaris (Ulbricht)
First flagellar segment less than 3.5 × longer than broad; flagellum with at least 50 segments; paler, propodeum more weakly areolated.
areolaris (Brauns)
First flagellar segment at least 3.5 × longer than broad; flagellum with less than 50 segments; darker, propodeum more distinctly areolated.

As stated by Oosterbroek (1978), the characters given by Gauld (1973) are not reliable for separation of these two species. While I have been able to gain some knowledge of infraspecific variation within *ocellaris*, it is quite likely that discovery of further *areolaris* material will further modify our concept of species differences within *Platophion*. Oosterbroek (loc. cit.) reasonably questions the validity of the two species here treated.

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